AN INVESTIGATION OF THE RELATIONSHIP BETWEEN REPRODUCTIVE PATTERNS AND PREDATION RISK FOR AMPHIPODS LIVING IN DIFFERENT HABITATS

A thesis submitted for the degree of Doctor of Philosophy of the Australian National University.

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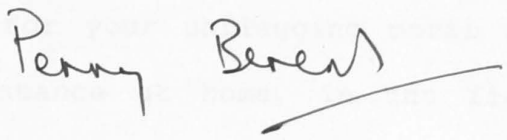
The research reported in this thesis was conducted by me except where explicitly acknowledged.



Penelope Berents

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Dedication

To Peter

Thank you for your encouragement to undertake this thesis, and for your unflagging moral support and enthusiastic assistance at home, in the field, in the lab and in preparing the thesis.

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Preface

This thesis is written as a series of five papers. Chapters 2 to 5 have been prepared as manuscripts to be submitted for publication. Therefore these chapters are in the style of the journal which is noted at the beginning of each chapter. Chapter 6 has been published and is presented as a reprint. An introduction (chapter 1) outlines the central questions addressed, and a discussion (chapter 7) synthesizes the results of the study. References to the papers in this thesis are made as citations (Berents, thesis papers a-d) and listed in the literature cited. Each chapter includes a reference section, tables and figures at the end of the text.

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A REVIEW OF AMPHIPOD LIFE HISTORIES

There have been many theoretical approaches to the study of life histories. Models have been proposed to explain iteroparity and semelparity (Murphy, 1968; Charnov and Schaffer, 1973; Bulmer, 1985), small and large eggs (Vance, 1973a and b; Perron and Carrier, 1981), and small and large broods (Lack, 1954; Cody, 1966; Price, 1974). Murphy (1968), Charnov and Schaffer (1973) and Bulmer (1985) proposed that iteroparity, or repeated reproduction, was advantageous if juvenile survival was uncertain. Vance (1973a) concluded that the most efficient egg sizes were at the extremes of egg size and Perron and Carrier (1981) modified the model to reflect Perron's observations that both unimodal or bimodal distributions of egg size were found in nature. Lack (1954) proposed that brood size in birds reflected the largest number of offspring that parents could feed but Cody (1966) argued that the energy that was available for reproduction had to be partitioned between egg production, predator avoidance and competition and this determined brood size. Price (1974) examined Lack's and Cody's hypotheses and concluded that brood size was determined by a combination of these factors. There have been numerous attempts to find a general theory for the evolution of life history patterns.

MacArthur & Wilson (1967) proposed the theory of r- and K- selection in response to observations of two distinct suites of life history traits observed in species subject to density-dependent and density-independent selection. The meaning of the terms r- and K- selection has since broadened (Pianka, 1970 and 1972) but Parry (1981) and Boyce (1984) recommended that r- and K- selection be used only as a model of density-dependent and density- independent selection as originally formulated. Stearns (1976) described r- selection as referring to the combination of large reproductive effort, many small young, early age at maturity and a short life, and K- selection as referring to the combination of small reproductive effort, few large young, late maturity, and a long life.

In a major review of life history studies, Stearns (1976) argued that age-specific mortality was a critical factor in predicting reproductive patterns. He proposed a theory called bet-hedging which predicts that the traits predicted by r- and K- selection will be reversed if

juvenile mortality is variable.

However, field-based studies show that data does not always fit the predictions of these hypotheses (Menge, 1974; Fenwick, 1984). There is a need in the continuing investigation of life histories for field based studies to gather empirical evidence and to test hypotheses and develop new ideas. I propose to test the predictions of an hypothesis which makes predictions about egg size and number in gammaridean amphipods.

Amphipods are well suited to life history studies because females brood their eggs in a brood pouch where egg development is completed. Egg size and number are easily measured, and there is no larval stage.

In the northern hemisphere the life histories of many amphipods have been studied. One approach to life history studies has been to make comparative studies of amphipod reproductive patterns for different species in the same habitat (Wildish, 1980; Borowsky, 1980; Moore, 1981; Sameoto, 1969; Skadsheim, 1982; 1984; Bregazzi, 1972; Kolding, 1981; Leineweber, 1985; Fenwick, 1985; Slattery,

1985), while others have compared reproductive patterns for the same genus or species in different localities or habitats (Steele, D H and V J Steele, 1969, 1972a, 1973 1975a, b, c,; Steele, D H 1976; Van Dolah, 1978; Kolding and Fenchel, 1981; Fredette and Diaz, 1986). Morino (1978), Nelson (1980) and Van Dolah and Bird (1980) tabulated life history data from many of these studies.

As a result of these studies a considerable amount of data exist about the reproductive patterns of amphipods in the northern hemisphere. Van Dolah and Bird (1980) reviewed the data in the literature and examined other collections in order to compare the reproductive patterns of twenty-six species of infaunal and epifaunal amphipods. They compared egg size and number for epifaunal and infaunal amphipods, and proposed the hypothesis that adult mortality risk is correlated positively with brood size and inversely with egg size. Van Dolah and Bird (1980) argued that epifaunal species of amphipods have more and smaller eggs than infaunal species, because of the increased adult mortality risk from predation, which is associated with epifaunal life. The advantage of smaller eggs for epifaunal amphipods is that smaller eggs develop

more quickly than larger eggs and therefore development time in the brood pouch is reduced. Amphipods brood their eggs, and therefore if there is a high risk of ovigerous females being eaten by predators, a short egg development time is advantageous. Adult mortality risk is therefore an important component of reproductive fitness.

Van Dolah and Bird's conclusions were based on data from the north-western Atlantic and they stressed that more rigorous testing of their hypothesis was required, "particularly among species reproducing at equivalent latitudes and seasons combined with conclusive evidence of differential risk of mortality".

Gammaridean amphipods are found in many habitats in the sea and reproductive patterns are diverse. Brood size, for example, varies from two to more than 400 eggs (Nelson, 1980). However, Van Dolah & Bird's hypothesis only considered infaunal and epifaunal amphipods. I propose to assess the applicability of the hypothesis on a wider scale.

Gammarideans in a number of families are commensal and

live in association with other invertebrates (Vader, 1972a and b; 1978; 1983). Endocommensal amphipods would be expected to be less at risk from predation than infaunal amphipods. Therefore, based on Van Dolah & Bird's model I predicted that commensal amphipods should have fewer and ~~smaller~~ larger eggs than infaunal amphipods. Vader (1983) found fecundity to be small for commensal amphipods and this evidence supported the hypothesis.

The aim of this study is to test the predictions of Van Dolah and Bird's hypothesis. I will describe and compare the reproductive patterns of two infaunal amphipods, an epifaunal amphipod and a commensal amphipod from the same locality, and assess the mortality risk from predation for these species. One of the infaunal species will be described as a part of the study. Van Dolah and Bird's hypothesis depends on two premises: firstly that epifaunal amphipods have more and smaller eggs than infaunal amphipods and secondly that there is a greater risk of predation in an epifaunal habitat. In order test the hypothesis, these two assumptions will be examined. This will provide the kind of test of the hypothesis that Van Dolah & Bird claimed was necessary.

The life histories of Australian amphipods are virtually unknown. There have only been three studies published which describe the life histories of Australian amphipods. Dexter (1985) examined some life history traits for four amphipod species from sandy beaches in south-eastern New South Wales. Lim & Williams (1971) studied Austrochiltonia subtenuis (Sayce) in a Victorian lake, and Smith and Williams (1983) have studied the reproductive patterns of Austrochiltonia australis (Sayce) and Pseudomoera gabrieli Sayce in freshwater creeks in southern Australia. This study will provide a detailed analysis of the life histories of four marine amphipods in Australia.

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LIFE HISTORIES AND POPULATION DYNAMICS OF INFAUNAL AMPHIPODS IN NEW SOUTH WALES.

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ABSTRACT

The life histories and population dynamics of the urohaustoriid amphipods Urohaustorius metungi Fearn-Wannan and Warragaia rintouli Berents were studied at Jervis Bay in New South Wales for eighteen months. Both species reproduced throughout the year and had short-lived summer generations and long-lived winter generations. Recruitment occurred every season and population densities were greatest in the summer. Brood size, egg size, sex ratios and generation times are reported in this study. Urohaustoriid reproductive strategies are compared with those of haustoriids in the northern hemisphere.

INTRODUCTION

Urohaustoriids are fossorial amphipods which only occur in Australia (Barnard and Drummond, 1982). They live in intertidal and subtidal sandy habitats. Closely-related families of fossorial amphipods are found in sandy habitats in other parts of the world. On the Atlantic coast of the USA, haustoriid amphipods are dominant species in sandy habitats (Croker, 1977), and the life histories of many have been studied (Croker, 1967; Dexter 1967; Sameoto 1969a & b; Dexter, 1971; Croker, 1977; Donn & Croker, 1983 & 1986). In contrast, there has been only one published study of urohaustoriid life histories in Australia (Dexter, 1985).

The aim of this study is to describe and compare the life histories and temporal patterns of abundance of two infaunal amphipod species in the family Urohaustoriidae. These life histories will also be compared with those of infaunal species in the northern hemisphere.

The species studied herein are Urohaustorius metunqi Fearn-Wannan and Warraqaia rintouli Berents. Urohaustorius

metungi is characteristic of dissipative and protected sand beaches, and reaches maximum abundance in clean sand (Dexter, 1983). This species is also found on intertidal sand flats in estuaries (Dexter, 1985), and occurs from Gippsland Lakes in Victoria to Moreton Bay in Queensland (Barnard & Drummond, 1982). Warragaia rintouli occurs subtidally in Jervis Bay and was described only recently (Berents, 1985). It has not been recorded from any other locality, and this is the first study of any aspect of its biology.

This report forms part of a larger work which seeks to assess Van Dolah & Bird's (1980) hypothesis which related differential reproductive patterns between infaunal and epifaunal amphipods to predation risk. They proposed the hypothesis "that adult mortality risk is correlated positively with egg number and inversely with egg size". Future papers (Berents, thesis papers b & d) will describe the life history of an epifaunal amphipod, and compare the risk of predation for infaunal and epifaunal amphipods.

METHODS

The study was carried out at Jervis Bay (35°05'S 150°45'E) on the south coast of New South Wales, Australia (Fig. 1). Jervis Bay is a large open bay with the foreshores dominated by sandy beaches.

Sampling Methods

Sampling was carried out each month from November 1981 until April 1983. The sampling programme was designed to yield at least 100 animals per month for each species, and was quantitative to allow estimates of monthly population densities. Different sampling and sorting methods were adopted for each habitat and are described below. Samples were preserved in 10% formalin and later transferred to 70% ethanol for sorting.

Sea surface temperatures were recorded daily at H.M.A.S. Creswell at Jervis Bay and these data were made available by the Australian Oceanographic Data Centre.

Sediment samples of approximately 70 ml were taken for grain-size analysis by standard sieve procedures (Folk & Ward, 1957). The mean grain size and graphic standard deviation (sorting) of each sediment sample were calculated.

Urohaustorius metunqi

The U. metunqi population was located on an intertidal sandflat about one kilometre upstream from the mouth of Currambene Creek (Fig. 1). The sandflat was stratified into three shore-parallel zones (upper, mid, lower) and randomly located cores taken from each. Each zone was 15 metres wide with the upper zone commencing at the edge of mangrove pneumatophores which formed the terrestrial margin of the sand flat. The lower zone could only be sampled seven times ie. during extreme low tides. Ten cores of 916cm3 and 11.8cm depth, were taken in each zone and washed through a 500 μm sieve. Specimens were sorted subsequently using a binocular microscope.

The vertical distribution of U. metunqi in the substratum was determined using a corer divided into five

sections each of 2.5 cm depth. The corer was pushed into the sediment and the sections of the core separated immediately, preserved and later sorted. The depth of the redox discontinuity was measured.

Emergence traps and plankton tows were used to determine whether U. metungi emerged from the sediment at night to swim in the water column. The design of the emergence traps was based on the recommendations of Youngbluth (1982). The traps consisted of a pyramid of polyethylene film attached to a square base of electrical conduit 0.5 x 0.5 metre, which was tethered so that it floated approximately 3 cm above the substratum. The cod-end consisted of a funnel which protruded into an inverted buoyant plastic bottle which floated 0.5 metres above the substratum. Holes of 1 cm diameter were cut into the sides and base of the bottle, and covered with 63μm mesh to allow water circulation. Animals which emerged from the sand were funnelled by the pyramid-shaped trap into the catch chamber. Each season traps were deployed in the evening and collected the following morning.

Plankton tows were made in spring and summer at high tide at the following times in the lunar month: 4 or 5 nights before the full moon, full moon, 4 or 5 nights after the full moon, and no moon.

Warragaia rintouli

Warragaia rintouli was sampled from a sandy bottom in eight metres of water off Moona Moona Creek (Fig. 1). Four replicate samples of sediment were taken from randomly located quadrats of 0.4 m2 using an airlift. Each sample was retained in a bag of 500 μm mesh which was then placed in 10% formalin, and stained in 1 % aqueous phloxine. Specimens were recovered from the sediment by elutriation and counted under stereomicroscopes. The sediment was inspected to ensure the removal of all amphipods.

The vertical distribution in the substratum was determined using the same divided corer as described for U. metungi. The corer was pushed into the sediment by a scuba diver and the core immediately brought to the surface, separated, preserved and later sorted.

Emergence traps and plankton tows were used to determine whether W. rintouli swam in the water column at night. The emergence traps were of the same design as those described for U. metunqi. Plankton tows were made at the surface by boat, and above the substratum by a scuba diver, at the same stages of the lunar month as for U. metunqi.

Laboratory Procedures

Amphipods were measured using an eyepiece graticule in a binocular microscope. The urohaustoriids were measured from the tip of the rostrum to the base of the telson along the mid-dorsal line. Unlike most gammarideans, urohaustoriids tend towards dorso-ventral compression and their total length is easily measured. The mean volume of ovigerous females was determined for five random samples of ovigerous females by displacement in a calibrated microvial. Each sample was measured three times and the mean calculated.

Sex was determined by the presence of the penial papillae on the sternum between the seventh peraeopods for

males, and the presence of oostegites for females. Amphipods lacking either of these secondary sexual characters were regarded as juveniles. Staining the amphipods with 1 % chlorazol black in lactophenol assisted in sex determination.

All eggs were removed from the brood pouch of every ovigerous female, measured, and the stage of embryonic development noted. Fish's (1975) classification system for the embryonic development of Bathyporeia pilosa Lindström and B. pelagica (Bate) was used as the basis for defining embryonic development of the study species. Fish's stages of development were defined as follows:

Stage 1: egg contains yolk and the germinal disc
Stage 2: appearance of the caudal furrow
Stage 3: rudimentary appendages visible
Stage 4: yolk reduced to a dorsal crescent, mid-gut caeca present, optic rudiments visible
Stage 5: beating heart visible
Stage 6: hatchlings in the brood pouch

The development stages of the embryo were easily distinguished using the binocular microscope. The longest

axis of the egg was measured by eye-piece micrometer for stages 1-5, and hatched young were measured as for adults. The volume of stage 1 eggs was calculated using the formula $V = 4/3\pi r3$, where r = maximum diameter ÷ 2 (Wildish, 1982).

Analysis of Data

Cohort Analysis

The monthly length-frequency data for each species represented a combined density of a mixture of cohorts. In order to identify cohorts it was necessary to estimate the frequency of the distribution. The frequency distributions were estimated using the non-parametric kernel density estimate (Silverman, 1981).

An alternative, and frequently used method for analysing length-frequency data, is the analysis of histograms (Dexter, 1971; Kamihira, 1981; Moore, 1981; Hiwatari & Kajihara, 1984; Dexter, 1985; Kemp et. al., 1985; Slattery, 1985). However an inherent problem with the use of histograms is that the shape, and therefore

interpretation, depends on the size of the interval selected, and on the location of the interval. Histograms can be useful for data that is strongly seasonal but both Van Dolah (1978) and La France & Ruber (1985) pointed out the difficulties of analysing data with extended or continuous reproduction. Another method is that proposed by Harding (1949) and Cassie (1954) involving the use of probability paper, (Mills, 1967; Wildish, 1980; Hughes, 1982; Fenwick, 1985) however, this method assumes a normal distribution. The use of the non-parametric kernel density estimate overcame these problems.

Cohorts of newly recruited juveniles were identified using both monthly length frequency density estimates, and data on reproductive activity. Population structure revealed peaks in juvenile recruitment which were identified in the density estimates. A cohort was defined as a group of individuals of the same age, which appeared in the population as juveniles, and could be identified in the population each month. The growth of the cohort was then traced in subsequent months. The modal length of each cohort was estimated each month from the density

estimates. Growth rates and generation time for each cohort were then calculated.

Life History Traits

Recruitment was defined as the appearance of juveniles in the population. Because amphipods do not have a larval stage, recruitment was represented by the emergence of juveniles from the brood pouch. Reproductive activity was defined as the percentage of females in the sample which were ovigerous. Mean reproductive activity was calculated each month.

Population density and sex ratios were calculated each month and the mean size of juveniles, females, ovigerous females and males calculated for the total sample.

Brood size was defined as the number of eggs in a brood and was calculated using only stage 1 eggs from synchronous broods. Brood mortality was defined as the number of eggs lost between stage 1 and stage 5, and was calculated by comparing the mean brood size of a brood of stage 1 eggs and the mean brood size of a brood of size 5

eggs. The use of stage 6 to estimate brood mortality may have given an overestimate of brood mortality because hatchlings can leave and re-enter the brood pouch (Croker, 1968; Sheader and Chia, 1970). Only broods with synchronous development of eggs were used in the calculation.

Reproductive effort has been estimated using energy budgets (Tinkle & Hadley, 1975) by calculating the ratio of brood to body biomass or joules (Williams, 1966; Gadgil & Bossert, 1970; Pianka, 1972; Tinkle & Hadley, 1973; King & Butler, 1985); and by calculating the ratio of gonad to somatic weight or calorific value (Hughes & Roberts, 1980; Perron, 1982; Fletcher, 1984; Gremare & Olive, 1986; Fletcher, 1988).

In life history studies of amphipods, the calculation of energy budgets, or the measurement of gonad and somatic weights has not been attempted. Fenwick (1984) measured the dry weight of the mean brood as a percentage of female dry weight but gave no information about methods used.

Reproductive effort in this study was estimated as the ratio of brood volume to female body volume expressed as a percentage (Pianka, 1978).

Regression analysis was used to define relationships between variables and Student's t test was used to compare means. In all cases confidence levels were set at 95 %.

RESULTS

The biology of Urohaustorius metungi

Urohaustorius metungi lived in well sorted, medium to coarse sand, with negligible silt-clay (Table 1). Urohaustorius metungi occurred across the entire sand flat from the edge of the mangrove zone to the water's edge at low tide (Fig. 2).

Water temperature ranged from a minimum of 13.4°C in July 1982 to a maximum of 23.6°C in February 1983 (Fig. 3).

Urohaustorius metungi was never caught in plankton samples or emergence traps. Neither males nor females

developed any of the modifications usually associated with swimming behaviour.

Most U. metunqi occurred above the redox discontinuity in the top five cms of the sediment (Table 2). At a point five metres from the terrestrial margin of the sand flat, 96.3 ± 3.7 % of U. metunqi lived in the top 2.5 cm, and 20 metres from the terrestrial margin of the sand flat 100 ± 0 % lived in the top 2.5 cm.

Reproductive Activity and Recruitment

Ovigerous females occurred in the population throughout the year, but reproductive activity was not constant (Fig. 4). Reproductive activity was greatest in the autumn sample of April 1982 and least in the summer sample of December 1982.

Ten cohorts (A-J, Figs 5 & 6) were traced from November 1981 to March 1983 (Table 3). Five of these (A-E) were traced for the life span of the cohort. There were up to five cohorts in the population simultaneously. In summer there were two or three cohorts, but in winter

there were three or four. In spring five cohorts were present. The sequence of recruitment of these cohorts was as follows.

At the commencement of sampling in November 1981 two cohorts (A & B) were present in the population. In December 1981 early summer recruitment began with cohort C, which was the offspring of cohorts A and B. By the end of summer cohort A had died, and cohort B was represented by a few large animals.

The autumn peak in reproductive activity produced two cohorts. Autumn cohort D appeared in March 1982, and in April 1982 a larger recruitment was apparent (cohort E). Although both cohorts were offspring of summer cohort C, they were discernible on the density distribution throughout their life spans.

With the onset of winter, reproductive activity remained constant with almost 12 percent of females carrying eggs. The first individuals of winter cohort F (which were the offspring of cohort D) appeared in June. Autumn cohort E was not then reproductively mature, and

summer cohort C was represented by large post-reproductive adults. A second winter cohort G appeared in July, which was also the offspring of autumn cohort D.

In spring, recruits of cohort H appeared in September and by October 1982, more than 50 % of the sample were juveniles. These were the offspring of autumn cohort E. Autumn cohort D was represented by a few large post-reproductive adults, and winter cohort F was approaching reproductive maturity.

In the following summer recruitment began with the appearance of summer cohort I, the offspring of winter cohort G. By the completion of sampling in March 1983, the first autumn recruits had appeared (cohort J).

Population Density and Structure

Urohaustorius metunqi was most abundant on the sand flat in early summer (December) of both years (Fig. 7). In January 1982 the population was dominated by females of cohort B (Fig. 8). A small number of post-reproductive cohort A and a few early juveniles from the summer

recruitment (cohort C) comprised the remainder of the population. The mean population density decreased five fold between December 1981 and February 1982. At this time, few of cohort B had survived and the autumn recruitment had not commenced.

Mean population density increased throughout autumn with the recruitment of juveniles in March (cohort D) and April (cohort E). Density then decreased sharply in June when the autumn cohorts (D and E) were present. Cohort D had reached reproductive maturity and cohort E was approaching maturity. The winter recruitment of juveniles (cohort F) had also commenced.

By July 1982, however, mean population density had returned to the levels of autumn presumably due to the winter recruitment of juveniles. Density remained stable until September, after which sharp increases, due to spring recruitment, occurred until December. The population in December was again dominated by the spring cohorts. Subsequently, the population followed the same pattern as that observed for the previous year's summer with a decrease in numbers.

Size Ranges

The biggest U. metungi recorded were males of 4.96 mm, and the mean length of males was 2.81 mm (Table 5). Hatchlings left the brood pouch from 0.92 mm in length although the mean length of hatchlings in the brood pouch was 0.96 mm. Penial processes were first discernible in males of 1.10 mm and oostegal buds first discernible in females of 1.46 mm, although juveniles up to 2.20 mm were noted. The smallest ovigerous females were 2.80 mm. Two specimens were recorded at this size and each carried three eggs. There was some size overlap between juveniles, and amphipods with secondary sexual characters.

The mean volume of ovigerous females was 3.64×10^{-3} ml ($n = 20$, 1 SE = 0.365×10^{-3}).

Sex Ratios

The ratio of males to females fluctuated from 0.7 to 1.7 (Fig. 9) but over the entire sampling period the ratio was 0.9. On six occasions there were more females than

males, and the greatest domination in favour of females occurred in November 1981, January 1982, April 1982, and October 1982. On three occasions, June 1982, January 1983 and March 1983, there were more males than females.

Embryonic Development

Embryonic development is described for Warragaia rintouli. The same pattern of development was observed for U. metungi except that the appearance of a caudal furrow could be distinguished. This characteristic was used to distinguish stage 2 embryos.

Brood Size and Brood Mortality

The brood size for U. metungi varied from one to twelve eggs with a mean of 4.8 (1 SE = 0.74, n = 18) (Table 5).

Brood size was not correlated significantly with the length of the ovigerous female (r = 0.08, n = 80) (Fig. 10). Large females often carried only one egg.

All broods did not have synchronous development. Thirty percent of broods contained embryos at more than one stage of development and more than two successive stages of development were found in 3.8 % of broods.

The mean size of a brood of stage 1 eggs was 4.72 eggs, and the mean size of a brood of stage 5 eggs was 3.0 eggs (Table 5). This difference in brood size was not significant ($t = 0.923$, $df = 19$), and therefore brood mortality was not significant.

Egg Size and Brood Volume

The mean diameter of U. metungi eggs increased by 27.5 % from stage 1 (0.51 mm) to stage 5 (0.65 mm) (Table 6). The greatest increase in diameter between successive stages occurred between stages 4 and 5. The mean volume of stage 1 eggs was $7.47 \times 10^{-2} mm^3$ (1 SE = 2.743×10^{-3}, n = 74), which gave a brood volume of $3.53 \times 10^{-1} mm^3$ (Table 7).

Longevity and Time to Female Reproductive Maturity

The ~~generation time~~ life span of U. metungi varied with the season of recruitment (Table 8). The shortest ~~generation time~~ life span of 181 days was for cohort C which recruited in the summer. These summer recruits showed rapid growth to reach maturity in the same summer and then died during the following winter.

The longest ~~generation time~~ life span was a mean of 231 days for those cohorts (D and E) which were recruited in autumn, reached maturity in autumn and winter, and then died the following spring.

The time taken for females to reach reproductive maturity also varied with the timing of recruitment (Table 8). Summer recruits (cohort C) reached reproductive maturity in 58 days but the cohort recruited in spring (cohort H) reached reproductive maturity in 145 days.

The biology of Warragaia rintouli

Warragaia rintouli lived in sediment that was moderately well sorted to moderately sorted, medium to coarse sand with negligible silt-clay (Table 9).

Warragaia rintouli were not caught in plankton samples or emergence trap samples taken at different lunar and tidal phases. Neither males nor females developed any of the modifications usually associated with swimming behaviour, such as elongate antennae, large eyes or setose uropods. Phoxocephalids and lysianassoids, which were modified for swimming, were abundant in these samples.

Most W. rintouli lived just below the sediment surface with a mean of 61.2 % of the total number in the core occurring in the top 2.5 cms, and 87.6 % in the top 5 cms (Table 10).

Reproductive Activity and Recruitment

Ovigerous females were present every month except one (Fig. 4). Warragaia rintouli reached maximum levels of

reproductive activity in the late winter and early spring (August September 1982) with more than 25 % of females carrying eggs. This peak in reproductive activity was followed by maximum recruitment in spring.

In October 1982, there were no ovigerous females in the population, but reproductive activity again exceeded 25% in February 1983.

Thirteen cohorts (A-M, Figs 6 & 11) were traced during the study from November 1981 to April 1983 and seven of these were followed for the lifespan of the cohort (Table 11). There were up to six cohorts in the population simultaneously. The sequence of recruitment was as follows.

At the commencement of sampling in November 1981, four cohorts were present in the population. Of these, cohort B dominated the density distribution and cohort A was represented by a few large individuals. Cohort C had not reached reproductive maturity and spring recruits had appeared (cohort D). Cohort D was the offspring of cohorts A and B. In both November and December 1981 more than 20

% of the population were juveniles. Reproductive activity in December dropped following the recruitment of spring cohort D.

In January and February 1982 there were problems in locating the correct sampling site and the density distribution was not reliable, because of a small sample size.

By autumn, cohort D, which was reproductively mature, dominated the density distribution and autumn recruits (the offspring of spring cohort D) appeared in April 1982 (cohort E). In late autumn and into winter reproductive activity increased and winter recruits appeared in June (cohort G) and July (cohort H). Cohort G was the offspring of cohorts D and E, and cohort H was the offspring of autumn cohorts E and F. Reproductive activity in August 1982 was the highest recorded for the sampling period. Autumn cohort F and winter cohort G produced spring recruits in September and October (cohort I). In October, spring cohort I comprised more than 40 % of the population, and there were no ovigerous females in the population.

In early summer reproductive activity increased and more than 15 % of females were ovigerous throughout the summer. Three summer cohorts were produced: cohort J offspring of autumn cohort F and winter cohorts G and H; cohort K offspring of winter cohorts G and H and spring cohort I; cohort L offspring of spring cohort I and summer cohort J.

Autumn recruits appeared in April 1983 (cohort M) as the summer cohorts K and L became reproductively mature. At the completion of sampling in April 1983 reproductive activity had dropped to less than 10 % and this reflected the pattern of April 1982.

Population Density and Structure

Warragaia rintouli was most abundant in late summer (Fig. 7) when the sample was dominated by adults of the early summer cohort J (Fig. 8).

Mean population density for the previous summer (1981-82) was confounded by the unreliable samples for

January and February 1982 because of uncertainty in locating the study site. However, in March 1982 the sample was dominated by the spring cohort (cohort D). Autumn recruitment commenced in the following month, and the mean population density increased. For the next six months, until early spring, mean population density was maintained and during this period five cohorts were produced. In July the proportion of juveniles in the sample exceeded 20 %.

By the middle of spring the proportion of juveniles in sample was at its yearly maximum following the spring recruitment. The adult population comprised the two winter cohorts (G and H) and the autumn cohort (F).

High mean population densities were maintained throughout the summer of 1982-83 until early autumn. Although mean population densities were relatively high throughout this period, there was a steady decrease in the mean density from the February maximum. There were some recruits to the population, but juveniles comprised less than 22 % of the sample throughout this period.

By mid-autumn mean population density had dropped. The population was dominated by the last of the three summer cohorts (cohort L) while the earlier summer cohorts (J and K) were represented by a few large females. Autumn recruitment (cohort M) had commenced, but only 7.5 % of the sample were juveniles.

Size Range

The largest W. rintouli were females of 2.56 mm with fully developed oostegites but without a brood (Table 12). The largest ovigerous female was 2.36 mm while males reached a maximum size of 2.04 mm. Penial processes were first discernible on males from 1.04 mm and oostegal buds appeared on females from 1.10 mm.

The mean volume of ovigerous females was 0.33×10^{-3}ml ($n = 73$, 1 SE = 0.036×10^{-3}).

Sex Ratios

The sex ratio of Warragaia rintouli fluctuated from 0.7 to 1.5 (Fig. 9) but over the entire sampling period

the ratio was 0.9. In autumn and winter there tended to be more females than males, and in spring and summer there were fewer females than males.

Embryonic Development

The first stage of embryonic development was the same as that illustrated by Fish (1975) in which the egg contained dividing yolk cells. The caudal furrow could not be distinguished in W. rintouli but limb buds were discernible at stage 3 and the yolk was sometimes restricted to a comma-shaped area as described by Fish (1975). Stage 4 embryos showed segmentation of the body, and sometimes the antennae and the urosome could be distinguished. In stage 5 embryos the articles of the appendages could be distinguished, and the sixth stage was hatched young in the marsupium.

Brood Size and Brood Mortality

Warragaia rintouli carried from one to seven eggs, with a mean of 1.9 eggs per ovigerous female (1 SE = 0.17, n = 52). The mean brood size varied seasonally and larger

mean brood size coincided with the spring peak in reproductive activity (Fig. 12)

Brood mortality was significant with a 32.5 % decrease in brood size from stage 1 broods (1.9 eggs) to stage 5 broods (1.3 eggs), ($t = 2.751$, effective df = 53) (Table 5).

Eggs within a brood did not all show synchronous development, and 12.7 % contained embryos at more than one stage of development. In 2.6 % of all broods more than two successive stages of development were found within a brood.

There was a significant correlation between brood size and the length of the ovigerous female ($y = 2.5x-2.6$, $r = 0.3844$, $n = 51$) (Fig. 10).

Egg Size and Brood Volume

The mean diameter of W. rintouli eggs increased by 45.5 % from stage 1 (0.33mm) to stage 5 (0.48m) (Table 6). The greatest increase in diameter between successive

stages occurred between stage 1 and stage 2. The mean volume of stage 1 eggs was 1.95 x 10^{-2} mm^3 (1 SE = 4.94 x 10^{-4}, n = 97) which gave a brood volume of 3.78 x 10^{-2} mm^3 (Table 7).

Longevity and Time to Female Reproductive Maturity

The ~~generation time~~ life span and the time for females to reach reproductive maturity for W. rintouli varied according to the season of recruitment (Table 13). Summer recruits had the shortest ~~generation time~~ life span of 123 days (cohort J) and winter recruits (cohorts G & H) had the longest ~~generation~~ life span time of 227 days. Autumn recruits (cohorts E & F) reached reproductive maturity in autumn and winter in a mean time of 34 days. The longest time to reproductive maturity was 76 days for the spring cohorts (D & I) which reached maturity in summer.

DISCUSSION

The life histories of Urohaustorius metungi and Warragaia rintouli followed similar patterns. They were both multivoltine with continuous reproduction. In both

species, cohorts recruited at different times of the year had different generation times, growth rates and time to reach female maturity. The summer generation was short-lived (about five months for U. metunqi and four months for W. rintouli) and females reached reproductive maturity the same summer, and then died the following autumn or winter. The longest lived generations of U. metunqi (about eight months) were recruited in autumn, reached reproductive maturity during the winter and died the following spring. The winter recruits of U. metunqi also lived for about eight months. The longest-lived generation of W. rintouli (about eight months) was recruited in winter, reached reproductive maturity by spring and died in summer.

Longevity

Generation times of up to 30 months have been reported for amphipods in the Bay of Fundy (Wildish, 1980) and more than three years for species in the South Orkney Islands (Bregazzi, 1972). In temperate zones, generation times were usually shorter (Sameoto,1969a & b; McBane & Croker, 1984) and there are many examples of amphipods with short-

lived summer generations and longer-lived winter generations of less than one year (Mills, 1967; Dexter, 1971; Moore, 1981; Hiwatari & Kajihara, 1984; Dexter, 1985; Fenwick, 1985; Dauvin, 1988). Cooler winter temperatures have been shown to inhibit growth in Ampelisca vadorum Mills and A. abdita Mills (Mills, 1967). Hughes (1982) also considered lower temperatures, rather than limited food supply, to cause slower winter growth rates in Proboscinotus loquax (Barnard) (as Doqielinotus loquax Barnard).

However, autumn 1982 was a period of slow growth for both U. metunqi and W. rintouli although water temperature was lower in mid-winter. This suggests that factors other than temperature affected growth rate, and food supply is an obvious possibility. Unfortunately it is not known what urohaustoriids feed on, and consequently the affects of food supply on growth rates cannot be assessed.

Population Dynamics

Population density for both species was greatest in spring and summer. This was a result of the spring

recruitment which dominated the population, and then matured quickly to produce offspring in summer.

Reproductive Activity

Both U. metunqi and W. rintouli had continuous reproduction and recruitment to the population every season. This pattern differed from most haustoriids, which had seasonal, rather than continuous reproductive activity (Sameoto, 1969a & b; Fish & Preece, 1970; Dexter, 1971; Fincham, 1971; Donn & Croker, 1986) although Eohaustorius sencillus Bousfield in Monterey Bay (Slattery, 1985), Bathyporeia nana Toulmond at the Isle of Man (Fincham, 1971) and B. pelaqica in Cardiganshire (Fish & Preece, 1970) had continuous reproduction. Dexter (1985) also found U. metunqi in Botany Bay to have continuous reproduction with reproductive activity never falling below 5 %. Other studies have found intraspecific variation in amphipod reproductive periods with latitude. Acanthohaustorius millsi Bousfield reproduced only in summer at Cape Cod (Sameoto, 1969b) but reproduced all year round in North Carolina (Dexter, 1967). Chaetoqammarus marinus Leach reproduced in spring and

summer in the Kattegat (Leineweber, 1985) but reproduced all year round in the Netherlands (Vlasblom, 1969) and France (van Maren, 1975). Such studies suggest that temperature or confounded factors such as day length and food availability may influence the duration of reproductive activity.

The males of some infaunal amphipods swim in the water column at night in search of females for reproduction. The males undergo morphological changes which enhance both their swimming and sensory abilities, including the development of elongate antennae, callynophores, calceoli, large eyes and setose uropods (Bousfield, 1970; Lowry & Stoddart, 1983; Lowry, 1986). This primitive pattern of reproduction (Bousfield, 1970) is found among the phoxocephalids (Barnard & Drummond, 1978), ampeliscids (Hastings, 1981) and lysianassoids (Fincham, 1974; Lowry & Stoddart, 1983). In contrast, haustoriids do not develop sexual dimorphism and they have not been collected in plankton samples (Croker, 1967; Sameoto, 1969a), except by Dexter (1971), who reported that numbers were insufficient for reproduction.

Neither Urohaustorius metunqi nor Warragaia rintouli were collected in plankton samples, and urohaustoriids do not develop sexual dimorphism as described for phoxocephalids, ampeliscids and lysianassoids. The reproductive behaviour of U. metunqi and W. rintouli remains undescribed, but the evidence suggests that they have evolved a more advanced strategy than the primitive strategy of swimming males as found in some infaunal amphipods.

Iteroparity

Ovigerous females of both species were present in the population every month (except one for W. rintouli). Each cohort had ovigerous females in the population for several months and the mean size of ovigerous females increased with the age of the cohort. These results suggest either that U. metunqi and W. rintouli produced a number of broods in the life of a cohort, or that egg development was slow and females carried the same brood during their period of reproductive maturity. Egg development time for urohaustoriids is not known, but Steele & Steele (1973) have shown that in Gammarus egg development, time is

correlated with temperature. Development time for amphipod eggs at temperatures exceeding 13°C, are less than 22 days (Steele & Steele, 1973; Fenwick, 1985), so U. metunqi and W. rintouli are probably iteroparous. Both semelparity and iteroparity are found among the haustoriids (Nelson, 1980).

It has been argued that iteroparity is selected in variable environments where juvenile survival is uncertain compared with adult survival (Murphy, 1968; Bulmer, 1985). However, Hirshfield & Tinkle (1975) and Grahame & Branch (1985) pointed out that in some extremely variable environments, semelparity would be selected if there was only a short season that was suitable for the survival of offspring.

Age-specific mortality rates for U. metunqi and W. rintouli are not known, although W. rintouli had significant brood mortality, and perhaps these species are iteroparous because juvenile mortality is high. It is unlikely that the environment at Jervis Bay represented the environmental extremes that would result in semelparity being advantageous.

Brood Mortality

Although the life histories of U. metungi and W. rintouli have similarities, there were also a number of differences. For example, brood mortality was significant in W. rintouli but not in U. metungi despite brood mortality of 36.4 %. However the sample size for U. metungi Stage 5 eggs was small, and the insignificant result may be because the type II error was large (Toft & Shea, 1983). Infaunal amphipods have been reported with both insignificant brood mortality (Bregazzi, 1972; Fenwick, 1985) and a high level of brood mortality of 45% (Kemp et al., 1985). Brood mortality can be affected by factors such as lack of fertilization, parasites, environmental extremes, accidental loss and consumption of eggs by the female (Sheader, 1983). Developing embryos were also susceptible to low oxygen levels and food availability (Shillaker and Moore, 1987).

Occasionally eggs which appeared to be unfertilized were found in the brood pouch of both study species. These eggs contained a yolky substance but there was no evidence

of cell division or differentiation. Accidental loss of eggs during sampling was unlikely because for both species the eggs were firmly enmeshed within the oostegites and were difficult to remove.

Embryonic Development

The direct development of gammarideans is easily traced by observing the changes in the embryo through the transparent egg membrane. Embryonic development has been described for haustoriids (Fish, 1975), aorids and corophiids (Moore, 1981), gammarids (Sheader and Chia, 1970), and lysianassoids (Bregazzi, 1972), and the pattern of development is similar in all families. Urohaustorius metungi and W. rintouli followed the same pattern.

Sex Ratios

In iteroparous amphipods, reproductive potential will be increased by a sex ratio favouring females if males are able to fertilize more than one female (Moore, 1981; Wildish, 1979). A number of haustoriid species have sex

ratios in favour of females (Croker, 1967; Sameoto,1969a; Fish and Preece, 1970).

In both urohaustoriids, females outnumbered males at some times of the year, and at other times males were dominant. For U. metunqi the times of greatest dominance of females coincided with peaks in reproductive activity. For W. rintouli, however, the sex ratio was 1:1 at the time of peak reproductive activity

Egg size, brood size and reproductive effort

Urohaustorius metunqi had larger eggs and a larger mean brood size than W. rintouli, however U. metunqi was also a larger species. Van Dolah and Bird (1980) listed egg sizes for fourteen infaunal amphipod species. Warraqaia rintouli had small eggs compared with other infaunal species but U. metunqi eggs were in the middle of the range of egg sizes listed by Van Dolah and Bird (1980).

Brood size is proportional to female size in many species of amphipods, including haustoriids, (Bone, 1972;

Hastings, 1981; Kamihira, 1981; Kolding & Fenchel, 1981; Dexter, 1985; LaFrance & Ruber, 1985; Donn & Croker, 1986; Fredette & Diaz, 1986). In W. rintouli, brood size was proportional to the size of the ovigerous female but the correlation was not significant for U. metungi. The largest broods were carried by large females but large females also carried only one egg. Consequently, large, old females may experience reproductive senility with reduced fecundity as found for Gammarus duebeni Lilljeborg (Kinne, 1961; Sheader & Chia, 1970).

Warragaia rintouli had a higher reproductive effort than U. metungi. This result is consistent with William's (1966) prediction that smaller, short-lived species have greater reproductive effort than larger long-lived species.

Both urohaustoriids and haustoriids are found in sandy habitats and both have evolved truncate, broad, fusiform bodies for fossorial life. Neither family has a swimming male as a part of its reproductive strategy. There are, however, some differences in other life history traits. Most haustoriids have seasonal reproduction and a number

are semelparous, whereas urohaustoriids have continuous reproduction and are probably iteroparous. Temperature is thought to be an important factor in determining the duration of periods of reproductive activity for amphipods (Steele & Steele, 1975; Morino 1978). Donn & Croker (1986) compared haustoriid life histories along the United States Atlantic coast and considered that the length of generations and reproductive periods increased for haustoriids in more southern locations. The reproductive patterns of urohaustoriids in other localities must be studied before conclusions can be reached about the influence that latitude and temperature have on urohaustoriid life history strategies.

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Table 1. Sediment analysis for Site 1 at Currambene Creek sandflat.

Date	Horizontal distance down sandflat m	Mean grain size ϕ	Sorting ϕ
Aug 1982	10	1.6	0.38
	20	1.4	0.41
	30	1.3	0.39
	35	1.2	0.37
	40	1.5	0.40
Oct 1982	5	1.5	0.44
	10	1.6	0.39
	15	1.6	0.42
	20	1.9	0.45
	25	1.2	0.40
Dec 1983	20	1.7	0.48
	20	1.7	0.44

Table 2. Vertical distribution of Urohaustorius metunqi in the sediment. The mean percentage of U. metunqi (± 1 SE) in each section of a divided corer.

Distance from terrestrial margin of sandflat (m)	n	Depth of redox discontinuity (cm)	Distance from sediment surface (cm) 0 - 2.5	2.5 - 5.0	5.0 - 7.5	7.5 - 10.0	10.0 - 12.5
5	3	3	96.3 ± 3.7	3.7 ± 3.7	0	0	0
10	3	5	47.9 ± 27.1	38.8 ± 20.0	11.1 ± 11.1	2.2 ± 2.2	0
20	2	5	100 ± 0	0	0	0	0
30	2	5	62.5 ± 37.5	37.5 ± 37.5	0	0	0

Table 3. Modal length of each cohort (mm) for Urohaustorius metungi. (Summer = Dec., Jan., Feb; autumn = Mar., Apr., May; winter = Jun., Jul., Aug; spring = Sep., Oct., Nov.)

	Cohort									
Date	A	B	C	D	E	F	G	H	I	J
Nov 1981	3.30	1.90								
Dec 1981	3.70	2.30	1.10							
Jan 1982	4.00	3.10	1.45							
Feb 1982		4.60	3.15							
Mar 1982			3.20	1.50						
Apr 1982			3.50	1.80	1.05					
May 1982			4.00	3.30	1.75					
Jun 1982			4.60	3.75	2.15	1.20				
Jul 1982				3.80	2.35	1.75	1.05			
Aug 1982				4.00	3.00	2.35	1.70			
Sep 1982				4.40	3.60	2.70	1.90	1.20		
Oct 1982				4.55	3.85	2.85	2.05	1.45		
Nov 1982					4.20	3.50	2.30	1.55		
Dec 1982					4.50	4.10	3.20	1.75		
Jan 1983						4.25	3.75	2.50	1.10	
Feb 1983							4.00	2.75	1.70	
Mar 1983							4.25	3.40	2.70	1.20

Table 4. Total length of Urohaustorius metungi at different stages of maturity.

	Size range (mm)	Mean	1 SE (mm)	n
Hatchlings in brood pouch	0.56 - 1.28	0.96	0.03	25
Juveniles	0.92 - 2.20	1.43	0.01	364
Females	1.46 - 4.24	2.84	0.06	456
Males	1.10 - 4.96	2.81	0.03	498
Ovigerous females	2.80 - 4.24	3.50	0.04	81

Table 5. Mean brood size (number of eggs) at each stage of embryonic development (synchronous broods only) for Urohaustorius metungi and Warragaia rintouli.

		Stage of embryonic Development							
		1	2	3	4	5	6	Brood mortality %	Sig.
Urohaustorius metungi		4.72	2.00	4.29	3.79	3.00	2.60	36.4	NS
	n	18	5	7	14	2	10		
Warragaia rintouli		1.94	2.67	1.92	1.73	1.31	1.33	32.5	*
	n	52	3	26	22	16	12		

Table 6. Mean diameter (mm) of eggs at each stage of embryonic development for urohaustoriid amphipods Urohaustorius metunqi and Warraqaia rintouli.

		Stage of embryonic development				
		1	2	3	4	5
Urohaustorius metunqi		0.51	0.52	0.54	0.59	0.65
	n	74	34	57	83	20
	1 SE	0.01	0.01	0.01	0.01	0.02
Warraqaia rintouli		0.33	0.40	0.43	0.47	0.48
	n	97	4	30	35	18
	1 SE	0.02	0.09	0.12	0.04	0.07

Table 7. Brood volume and reproductive effort for urohaustoriid amphipods Urohaustorius metungi and Warragaia rintouli.

	Mean egg volume ± 1 SE (mm^3)	Mean brood size (number of eggs)	Brood volume (mm^3)	Reproductive effort %
Urohaustorius metungi	0.0747	4.8	0.3525	9.7
1 SE	0.003	0.74		
Warragaia rintouli	0.0195	1.9	0.0378	11.5
1 SE	0.0005	0.17		

Table 8. Seasonal life history patterns of Urohaustorius metungi.

Recruitment	Female reproductive maturity	Mean time to maturity ± 1SE (days)	Death	Mean generation time ± 1SE (days)	Cohort
summer	summer	58 n=1	winter	181 n=1	C
autumn	autumn/winter	93 ± 23 n=2	spring	231 ± 3 n=2	D & E
winter	spring	129 ± 11 n=2	summer	223 ± 13 n=2	F & G
spring	summer	145 n=1			H

Table 9. Sediment analysis for Site 2 off Moona Moona Creek.

Date	Mean grain size ϕ	sorting ϕ
April 1982	1.1	0.89
July 1982	1.7	0.50
Dec 1983	1.8	0.68

Table 10. Vertical distribution of Warragaia rintouli in the sediment. The mean percentage of W. rintouli (±1 SE) in each section of a divided core, n = 7.

Distance from sediment surface (cms)				
0 - 2.5	2.5 - 5.0	5.0 - 7.5	7.5 - 10.0	10.0 - 12.5
61.2 ± 15.6	26.4 ± 9.8	3.9 ± 3.9	1.4 ± 1.4	7.1 ± 7.1

Table 11. Modal length of each cohort (mm) for Warragaia rintouli. (Summer = Dec., Jan., Feb; autumn = Mar., Apr., May; winter = Jun., Jul., Aug; spring = Sep., Oct., Nov.)

	Cohort												
Month	A	B	C	D	E	F	G	H	I	J	K	L	M
Nov 1981	2.20	1.65	1.15	0.80									
Dec 1981	2.30	2.00	1.43	1.00									
Mar 1982		2.15	1.98	1.43									
Apr 1982			2.10	1.56	0.85								
May 1982			2.20	2.00	1.53	1.05							
Jun 1982				2.15	1.55	1.23	0.90						
Jul 1982					2.00	1.48	1.10	0.80					
Aug 1982					2.27	1.85	1.55	0.97					
Sep 1982					2.40	2.00	1.63	1.15	0.77				
Oct 1982						2.16	1.71	1.40	1.15				
3 Dec 1982						2.25	1.80	1.60	1.25	0.93			
17 Dec 1982						2.37	2.15	1.80	1.53	1.15	0.82		
Jan 1983							2.28	2.00	1.77	1.45	0.97		
Feb 1983								2.25	2.03	1.60	1.10	0.91	
Mar 1983									2.25	2.05	1.56	1.08	
1 Apr 1983										2.20	1.97	1.50	0.90
29 Apr 1983										2.30	2.10	1.55	1.05

Table 12. Total length of Warragaia rintouli at different stages of maturity.

	Size range (mm)	Mean (mm)	1 SE	n
Hatchlings in brood pouch	0.30 - 0.66	0.56	0.07	13
Juveniles	0.76 - 1.42	1.07	0.01	305
Females	1.10 - 2.56	1.67	0.01	630
Males	1.04 - 2.04	1.49	0.05	846
Ovigerous females	1.40 - 2.36	2.00	0.04	168

Table 13. Seasonal life history patterns of Warragaia rintouli.

Recruitment	Female reproductive maturity	Mean time to ♀ maturity ± 1SE (days)	Death	Mean generation time ± 1SE (days)	Cohort
summer	summer	53 n=1	autumn	123 n=1	J
autumn	autumn/winter	34 ± 12 n=2	spring	179 ± 33 n=2	E & F
winter	winter/spring	68 ± 28 n=2	summer	227 ± 0 n=2	G & H
spring	summer	76 ± 7 n=2	autumn	187 ± 2 n=2	D & I

LEGENDS FOR FIGURES

Figure 1. Location of study sites at Jervis Bay, New South Wales, Australia. Site 1 was an intertidal sand flat in Currambene Creek; Site 2 was in eight metres depth off Moona Moona Creek.

Figure 2. The distribution of Urohaustorius metungi across the sandflat in Currambene Creek. The low zone was only sampled seven times at extreme low tides.

Figure 3. Mean water temperature in Jervis Bay, NSW, Australia.

Figure 4. Mean reproductive activity (the percentage of females that were ovigerous) and mean percentage of juveniles in monthly samples of Urohaustorius metungi (upper) and Warragaia rintouli (lower). Vertical bars indicate 1 SE. The replicates were combined for the first sample so standard error was not calculated.

Figure 5. Length frequency data for Urohaustorius metungi estimated by the non-parametric kernel density method. Dotted lines indicate the modal length of each cohort. (Summer = Dec., Jan., Feb; autumn = Mar., Apr., May; winter = June, July, Aug; spring = Sep., Oct., Nov.).

Figure 6. Modal length of cohorts of Urohaustorius metunqi (upper) and Warraqaia rintouli (lower). The size of reproductive females is indicated.

Figure 7. Mean population density (± 1 SE) of Urohaustorius metunqi (upper) and Warraqaia rintouli (lower). The replicates of the first sample of U. metunqi were combined so standard error was not calculated.

Figure 8. The percentage of males, females and juveniles in monthly samples of Urohaustorius metunqi (upper) and Warraqaia rintouli (lower).

Figure 9. The ratio of females and males of Urohaustorius metunqi (upper) and Warraqaia rintouli (lower). Samples of W. rintouli in January and February 1982 were too small to calculate sex ratios.

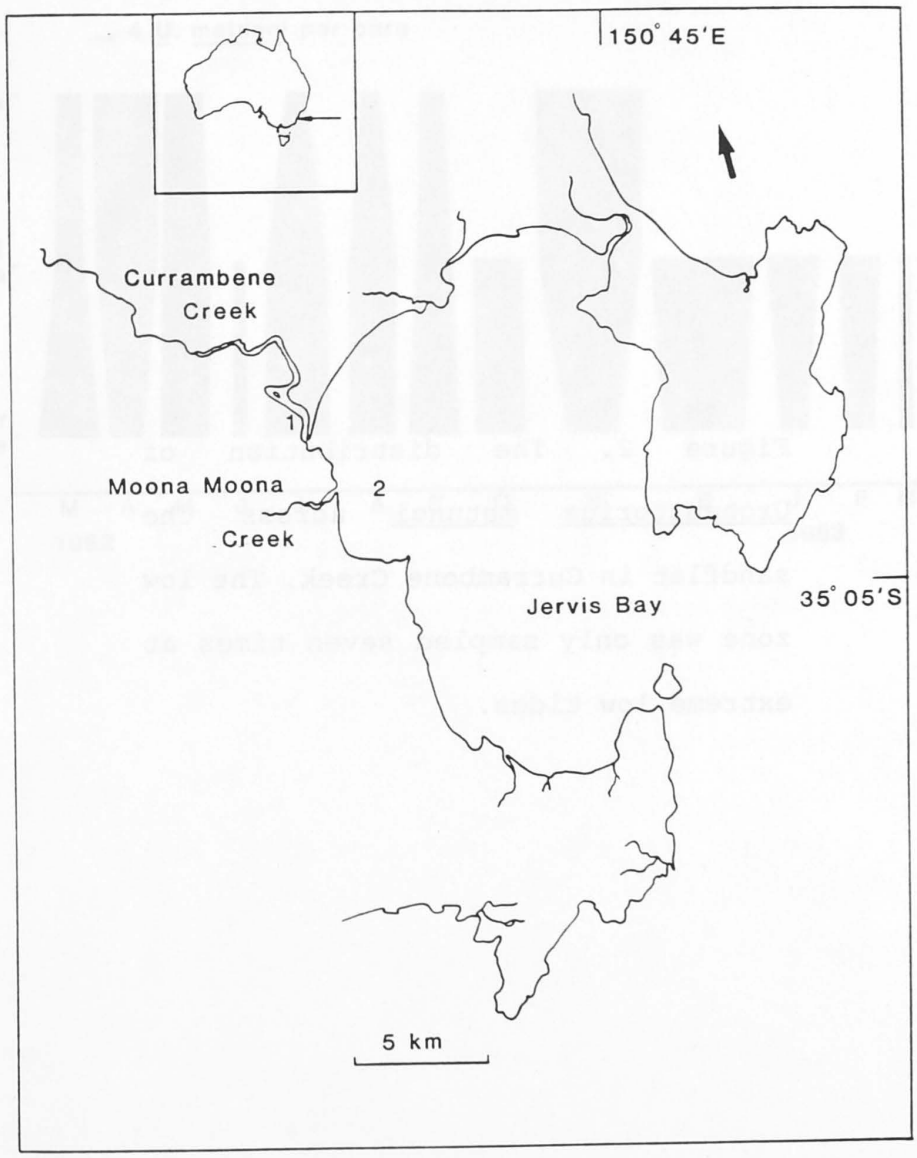
Figure 10. Brood size (number of eggs) and length of ovigerous females of Urohaustorius metunqi (upper) and Warraqaia rintouli (lower), showing significant linear regression for W. rintouli ($y = 2.5x-2.6$).

Figure 11. Length-frequency data for Warraqaia rintouli estimated by the non-parametric kernel density method. Dotted lines indicate the modal length of each cohort. The sample size in January and

February 1982 was too small for cohort analysis. (Summer = Dec., Jan., Feb; autumn = Mar., Apr., May; winter = June, July, Aug; spring = Sep., Oct., Nov.)

Figure 12. Mean brood size (± 1 SE), of synchronous stage 1 broods, for Warragaia rintouli.

Figure 1. Location of study sites at Jervis Bay, New South Wales, Australia. Site 1 was an intertidal sand flat in Currambene Creek; Site 2 was in eight metres depth off Moona Moona Creek.


150° 45'E
Currambene
Creek
1
Moona Moona
Creek
2
Jervis Bay
35° 05'S
5 km

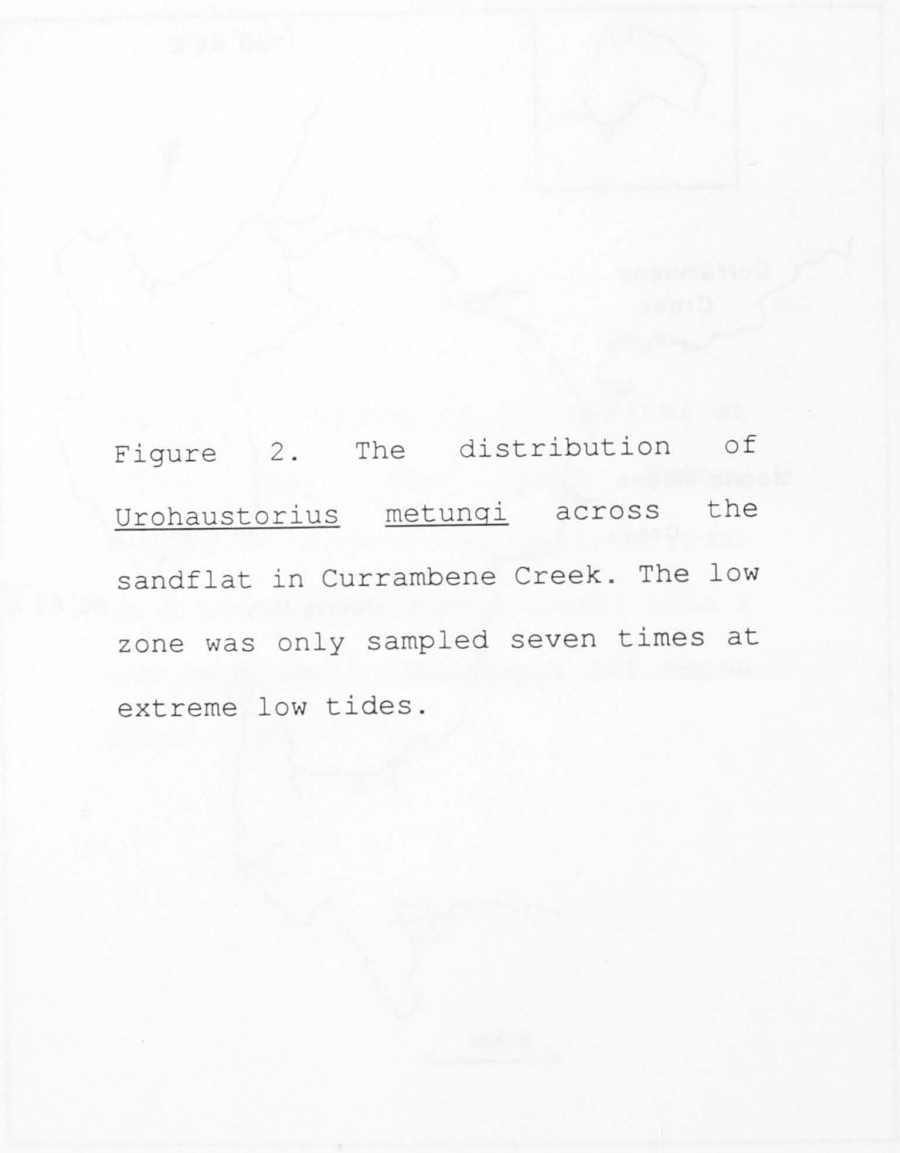


Figure 2. The distribution of Urohaustorius metungi across the sandflat in Currambene Creek. The low zone was only sampled seven times at extreme low tides.

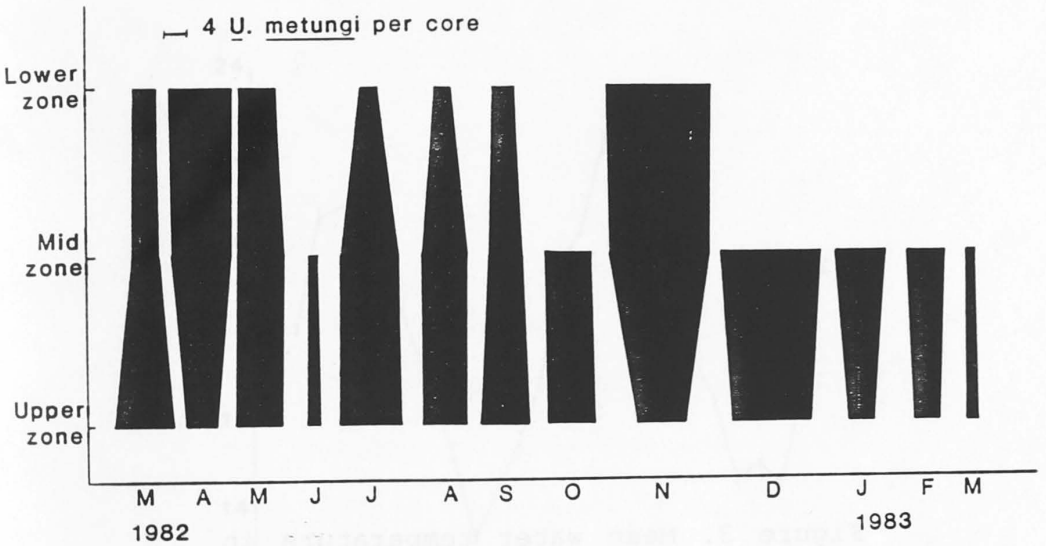

4 U. metungi per core
Lower zone
Mid zone
Upper zone
M A M J J A S O N D J F M
1982
1983

Figure 3. Mean water temperature in Jervis Bay, NSW, Australia.

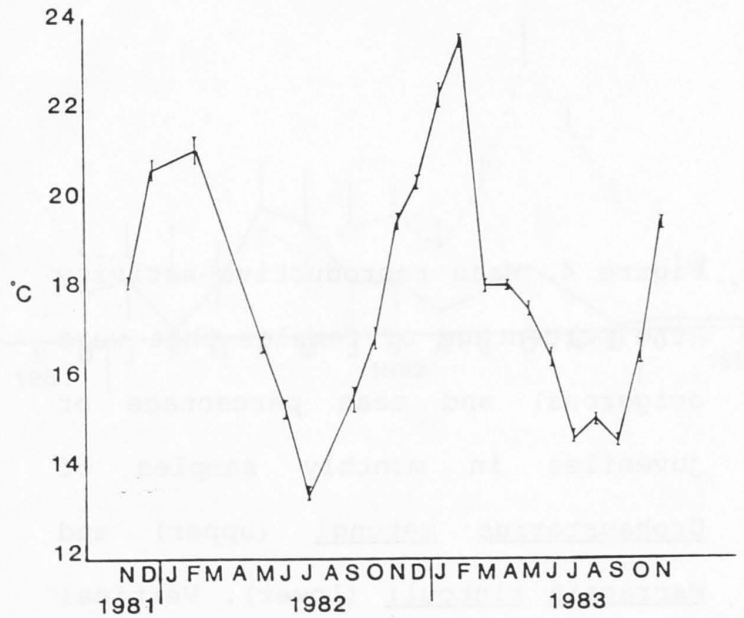
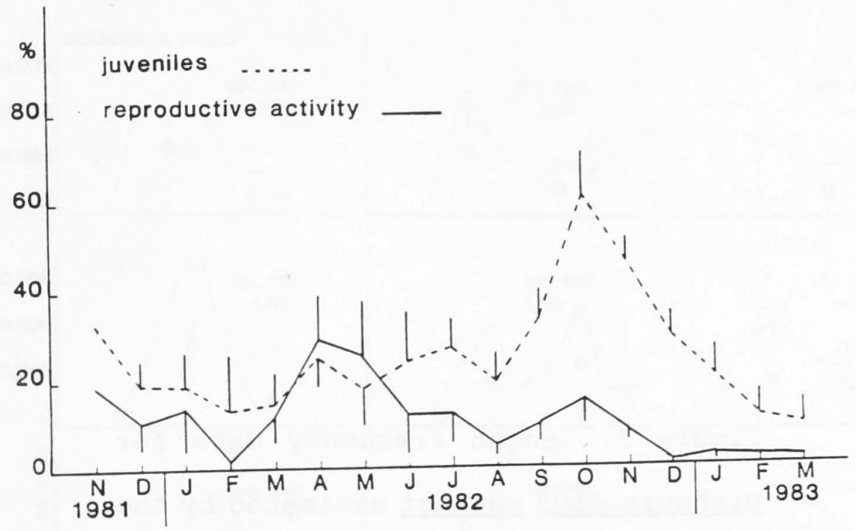

24
22
20
°C 18
16
14
12
N D J F M A M J J A S O N D J F M A M J J A S O N
1981
1982
1983

Figure 4. Mean reproductive activity (the percentage of females that were ovigerous) and mean percentage of juveniles in monthly samples of Urohaustorius metunqi (upper) and Warraqaia rintouli (lower). Vertical bars indicate 1 SE. The replicates were combined for the first sample so standard error was not calculated.


%
juveniles
reproductive activity
80
60
40
20
0
N D J F M A M J J A S O N D J F M
1981
1982
1983

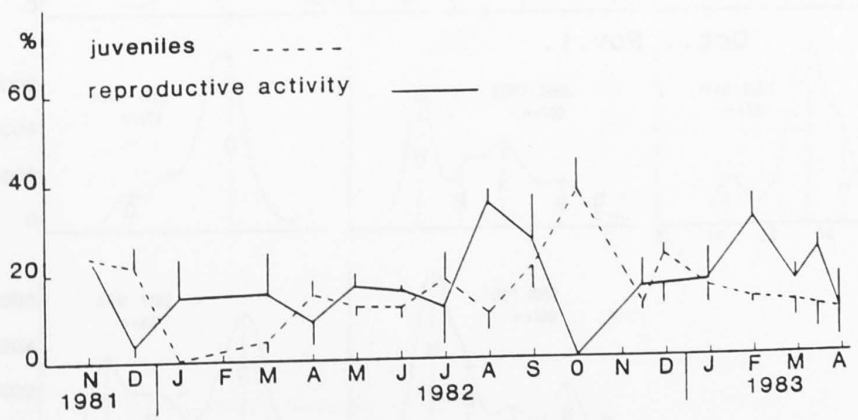
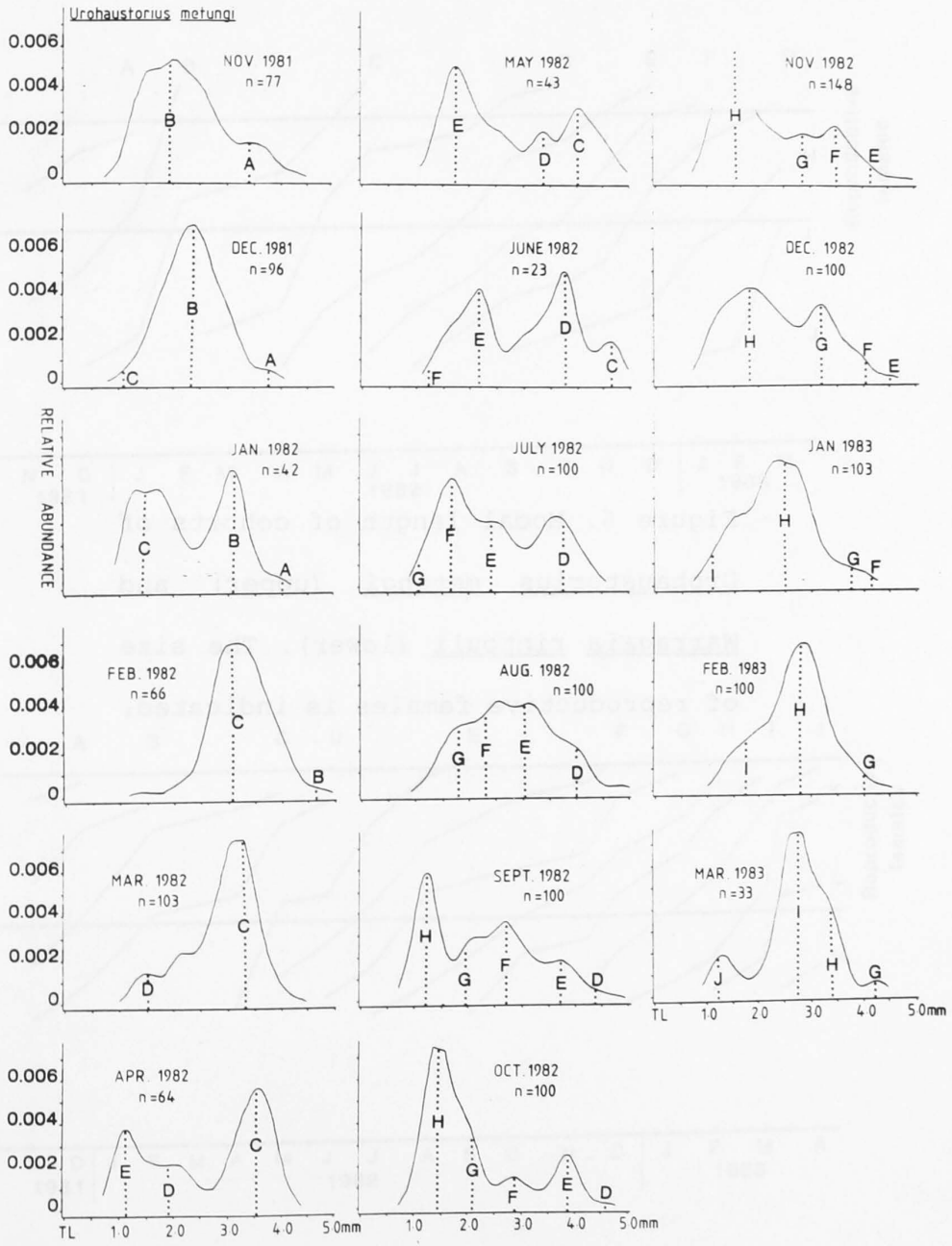

%
juveniles
reproductive activity
60
40
20
0
N D J F M A M J J A S O N D J F M A
1981
1982
1983

Figure 5. Length frequency data for Urohaustorius metunqi estimated by the non-parametric kernel density method. Dotted lines indicate the modal length of each cohort. (Summer = Dec., Jan., Feb; autumn = Mar., Apr., May; winter = June, July, Aug; spring = Sep., Oct., Nov.).


Urohaustorius metungi
RELATIVE ABUNDANCE
0.006
0.004
0.002
0
NOV. 1981 n=77
MAY 1982 n=43
NOV. 1982 n=148
DEC. 1981 n=96
JUNE 1982 n=23
DEC. 1982 n=100
JAN. 1982 n=42
JULY 1982 n=100
JAN. 1983 n=103
FEB. 1982 n=66
AUG. 1982 n=100
FEB. 1983 n=100
MAR. 1982 n=103
SEPT. 1982 n=100
MAR. 1983 n=33
APR. 1982 n=64
OCT. 1982 n=100
TL 1.0 2.0 3.0 4.0 5.0mm

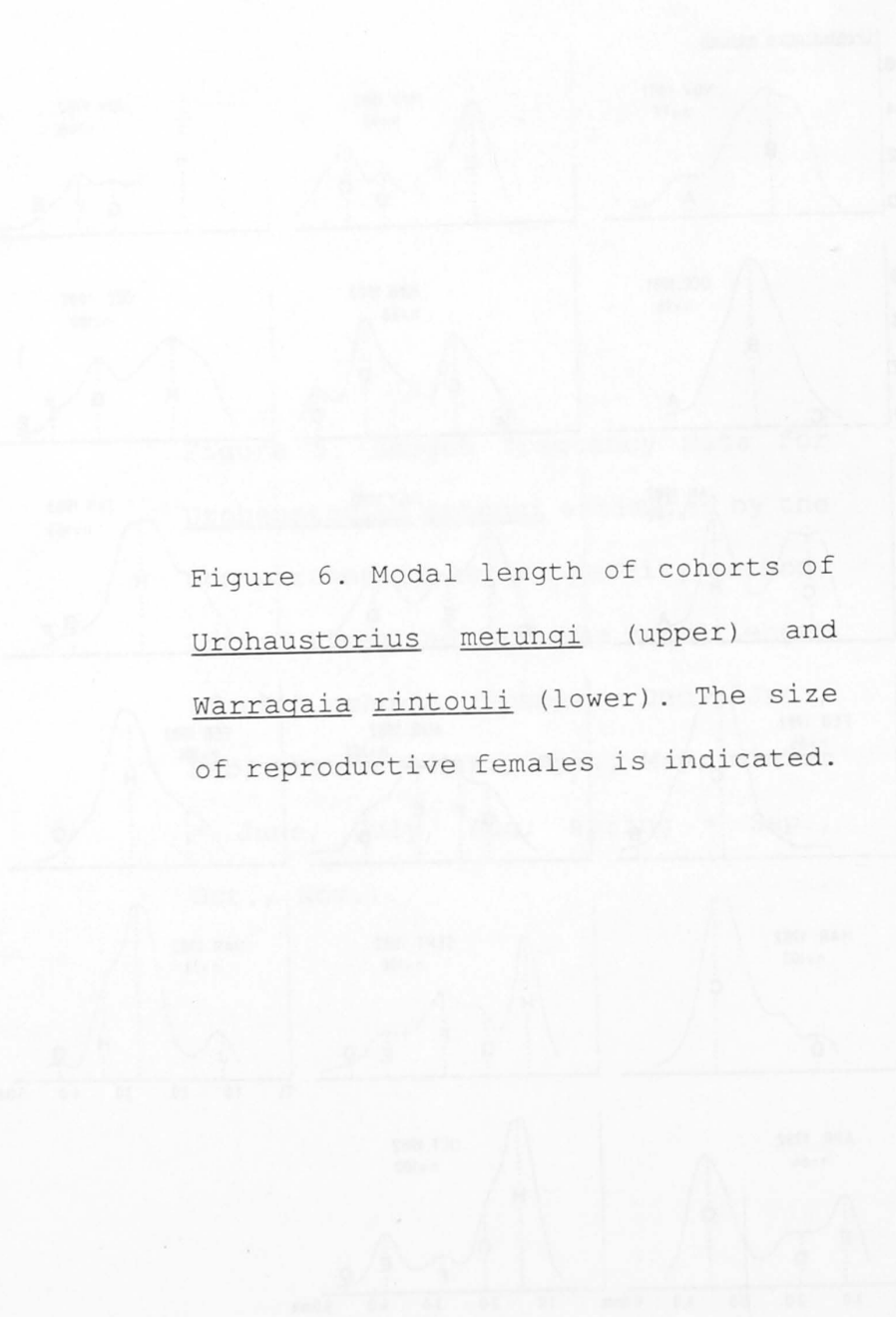
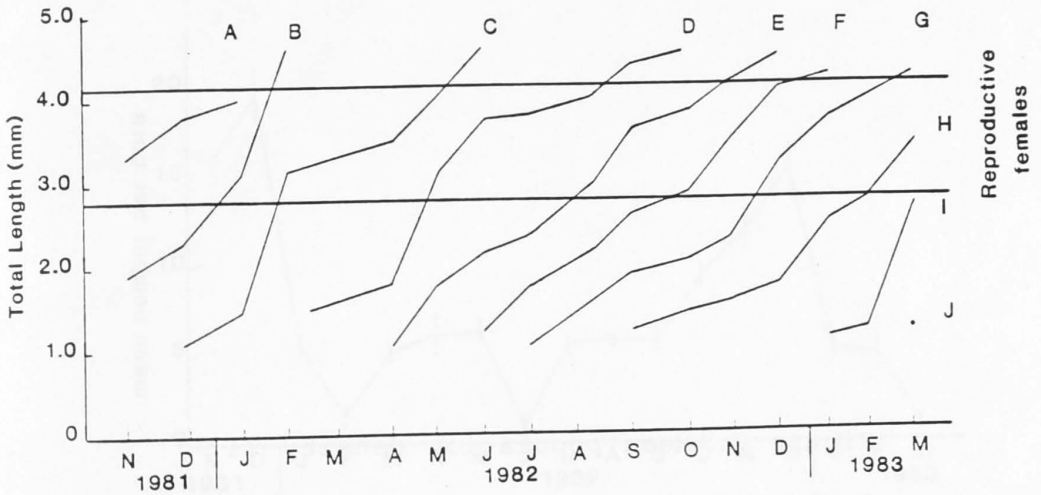
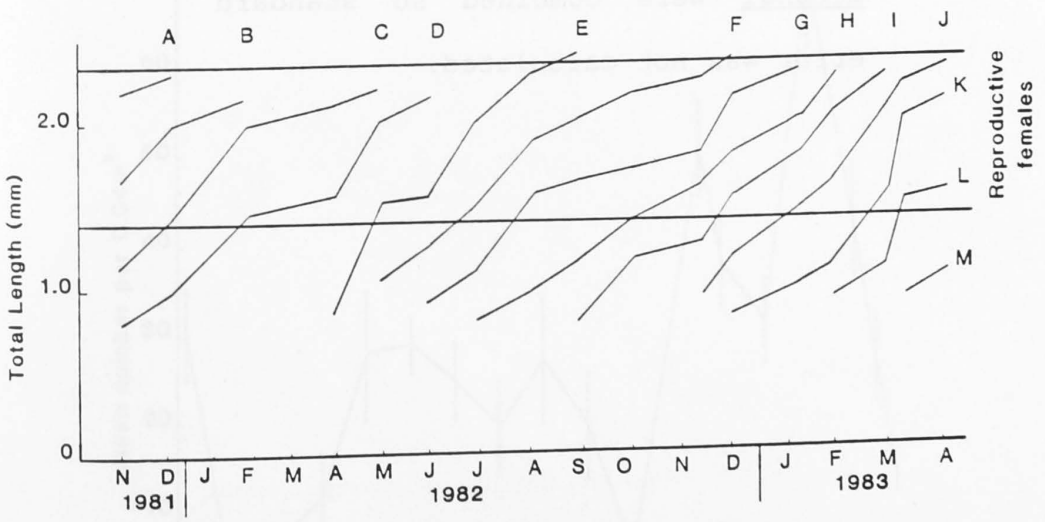


Figure 6. Modal length of cohorts of *Urohaustorius metungi* (upper) and *Warragaia rintouli* (lower). The size of reproductive females is indicated.


5.0
4.0
3.0
2.0
1.0
0
Total Length (mm)
A
B
C
D
E
F
G
H
I
J
Reproductive females
N D J F M A M J J A S O N D J F M
1981
1982
1983


2.0
1.0
0
Total Length (mm)
A
B
C
D
E
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H
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K
L
M
Reproductive females
N D J F M A M J J A S O N D J F M A
1981
1982
1983

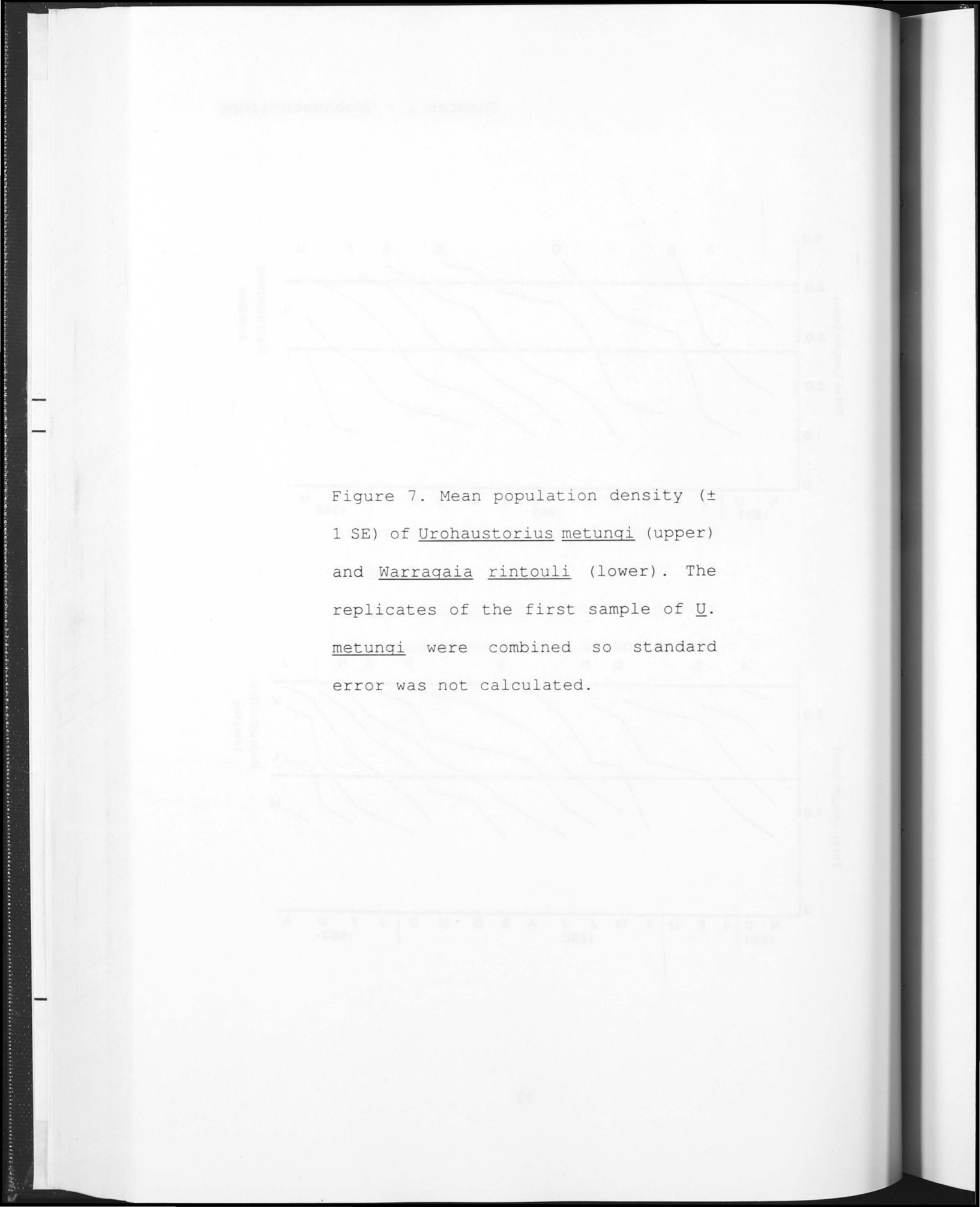
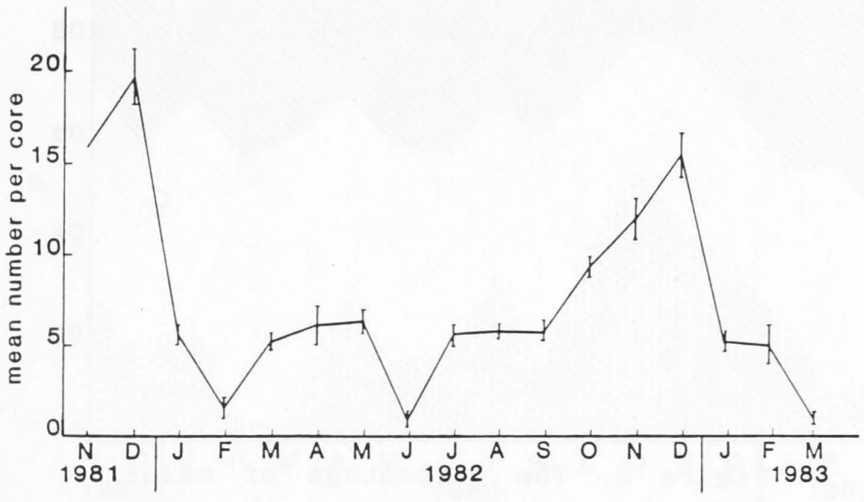
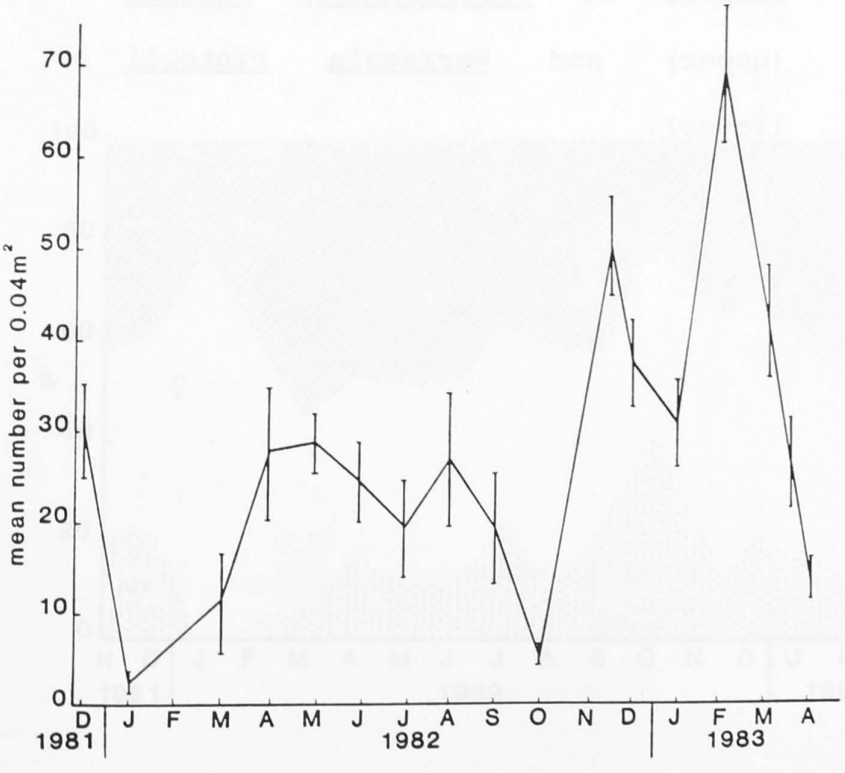


Figure 7. Mean population density (± 1 SE) of Urohaustorius metunqi (upper) and Warraqaia rintouli (lower). The replicates of the first sample of U. metunqi were combined so standard error was not calculated.


mean number per core
20
15
10
5
0
N D J F M A M J J A S O N D J F M
1981
1982
1983


mean number per 0.04m²
70
60
50
40
30
20
10
0
D J F M A M J J A S O N D J F M A
1981
1982
1983

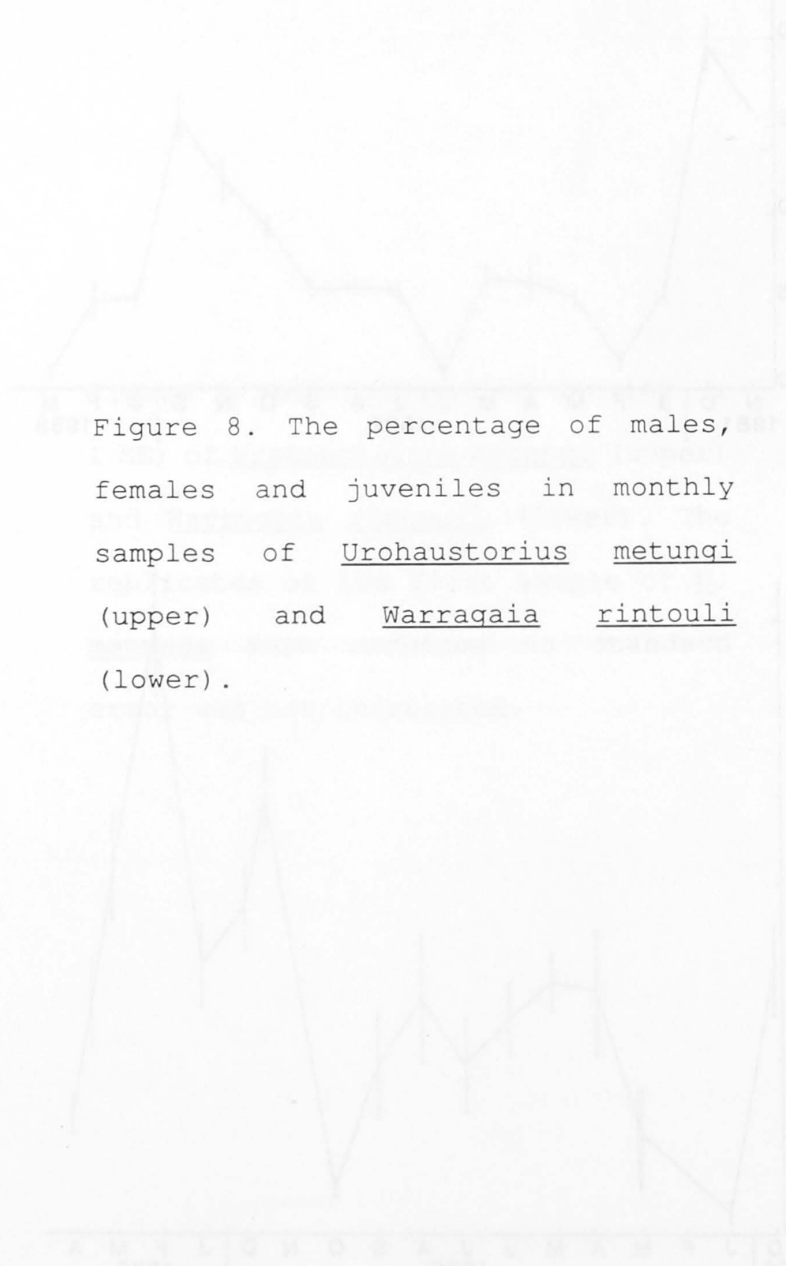
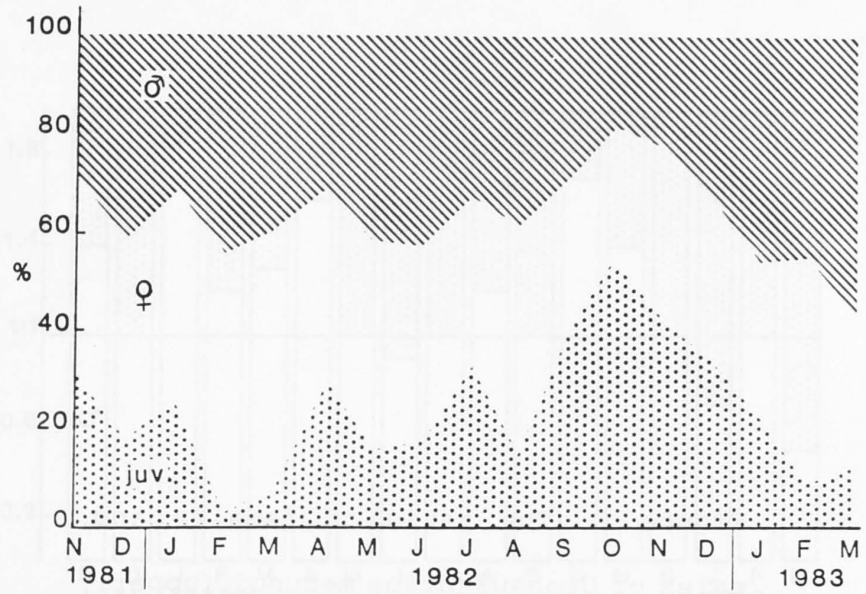
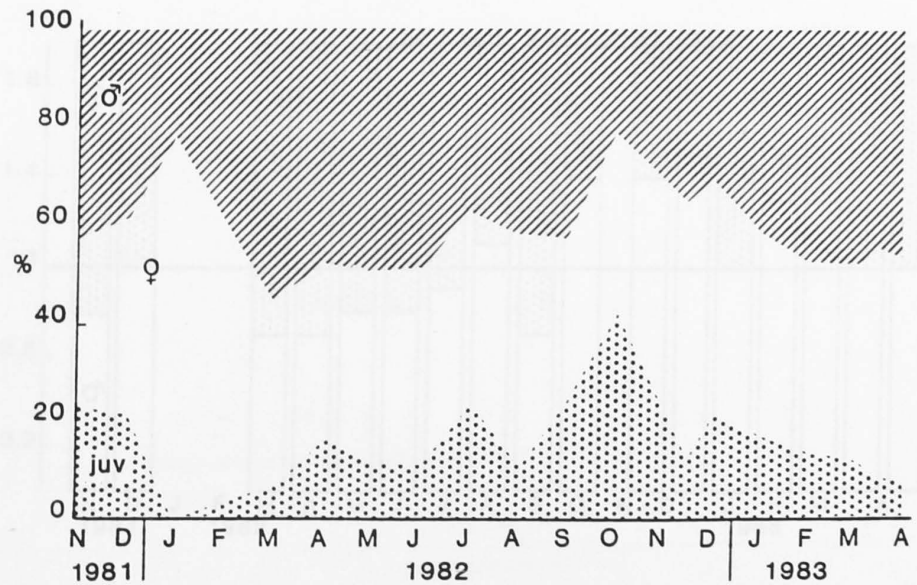


Figure 8. The percentage of males, females and juveniles in monthly samples of Urohaustorius metunqi (upper) and Warraqaia rintouli (lower).


100
80
60
%
40
20
0
♂
♀
juv.
N D J F M A M J J A S O N D J F M
1981
1982
1983


100
80
60
%
40
20
0
♂
♀
juv
N D J F M A M J J A S O N D J F M A
1981
1982
1983

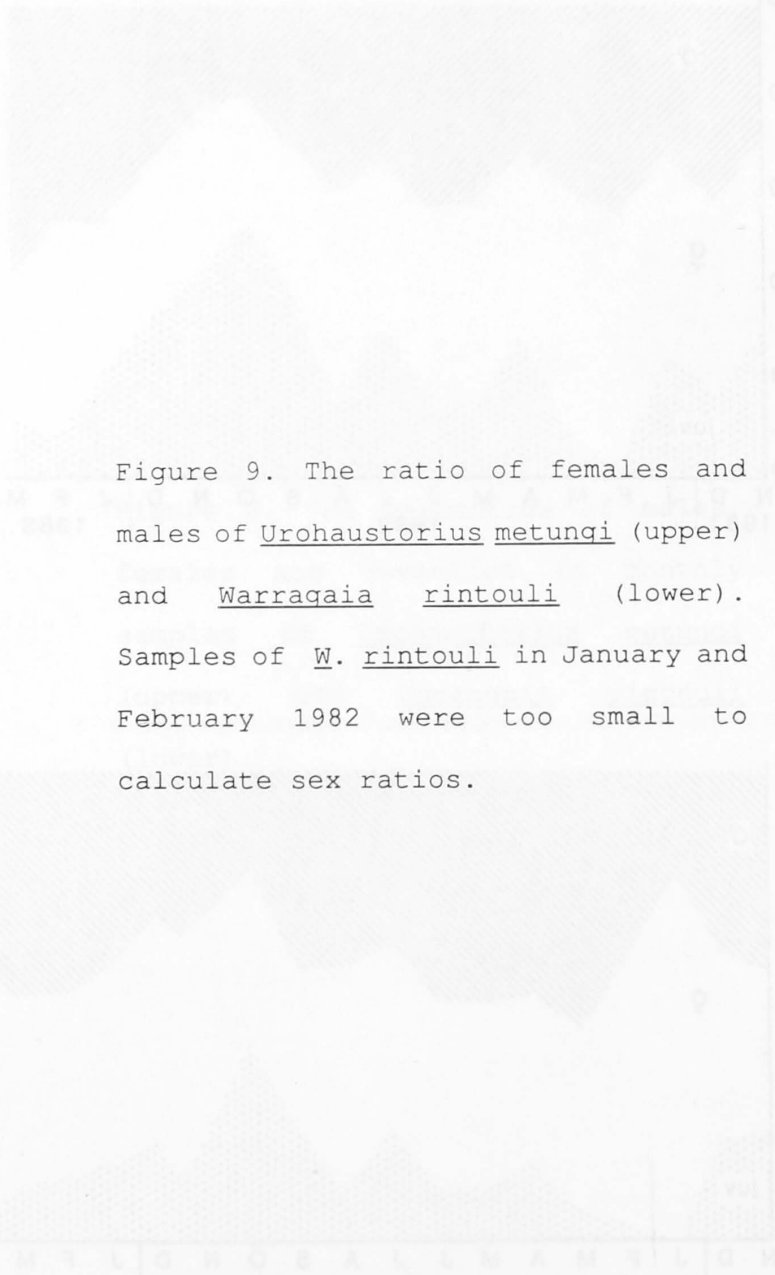
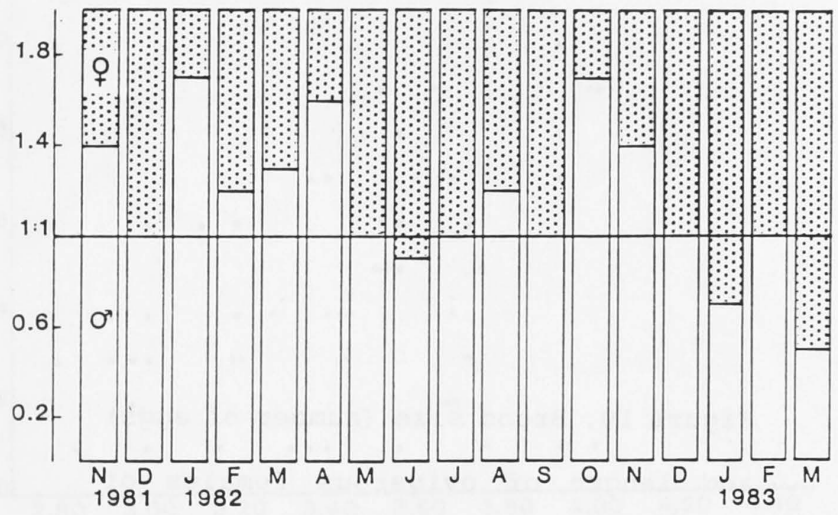


Figure 9. The ratio of females and males of Urohaustorius metunqi (upper) and Warraqaia rintouli (lower). Samples of W. rintouli in January and February 1982 were too small to calculate sex ratios.


1.8
1.4
1:1
0.6
0.2
♀
♂
N D J F M A M J J A S O N D J F M
1981 1982 1983

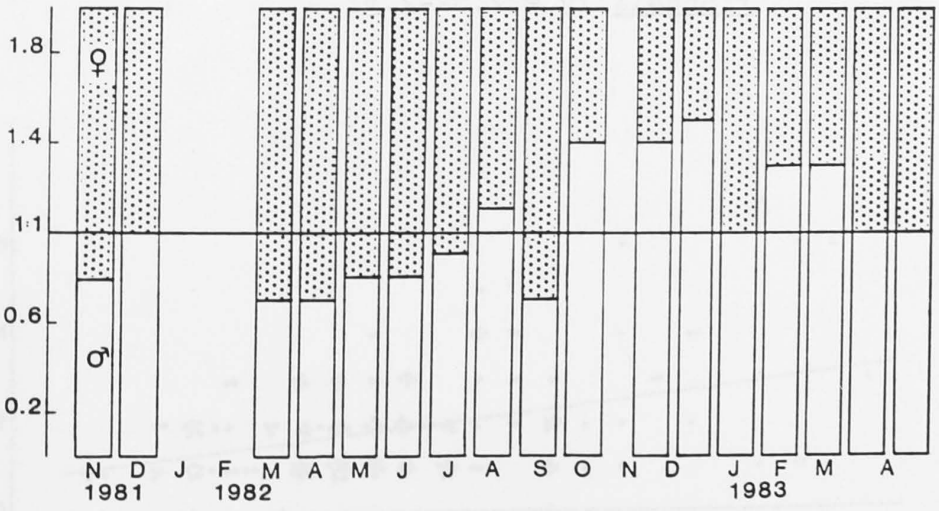
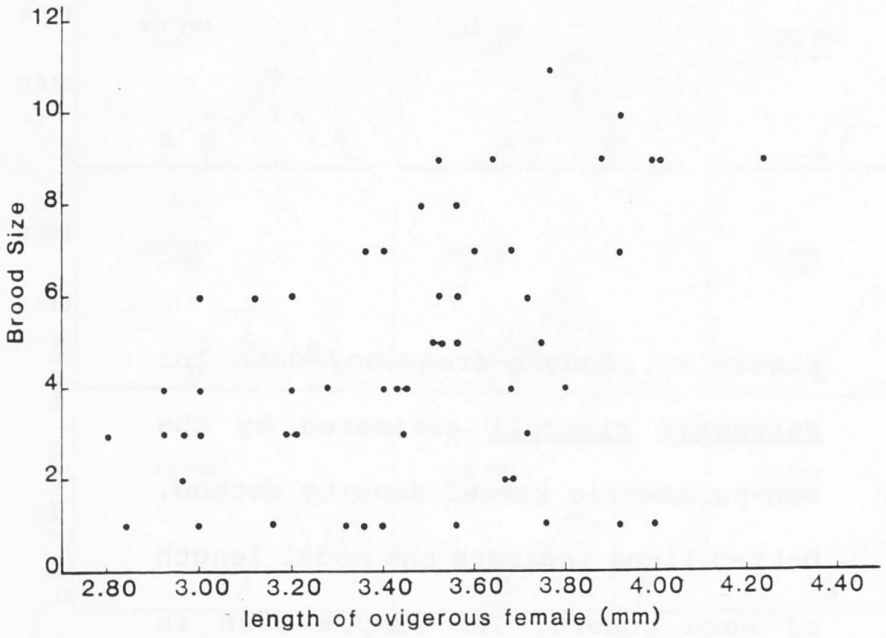

1.8
1.4
1:1
0.6
0.2
♀
♂
N D J F M A M J J A S O N D J F M A
1981 1982 1983

Figure 10. Brood size (number of eggs) and length of ovigerous females of Urohaustorius metungi (upper) and Warragaia rintouli (lower), showing significant linear regression for W. rintouli (y = 2.5x-2.6).


Brood Size
12
10
8
6
4
2
0
2.80
3.00
3.20
3.40
3.60
3.80
4.00
4.20
4.40
length of ovigerous female (mm)

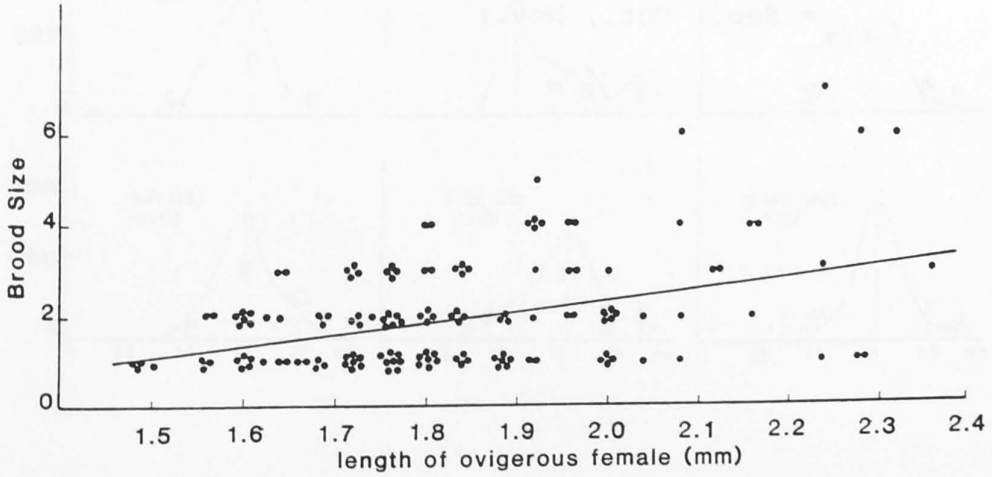
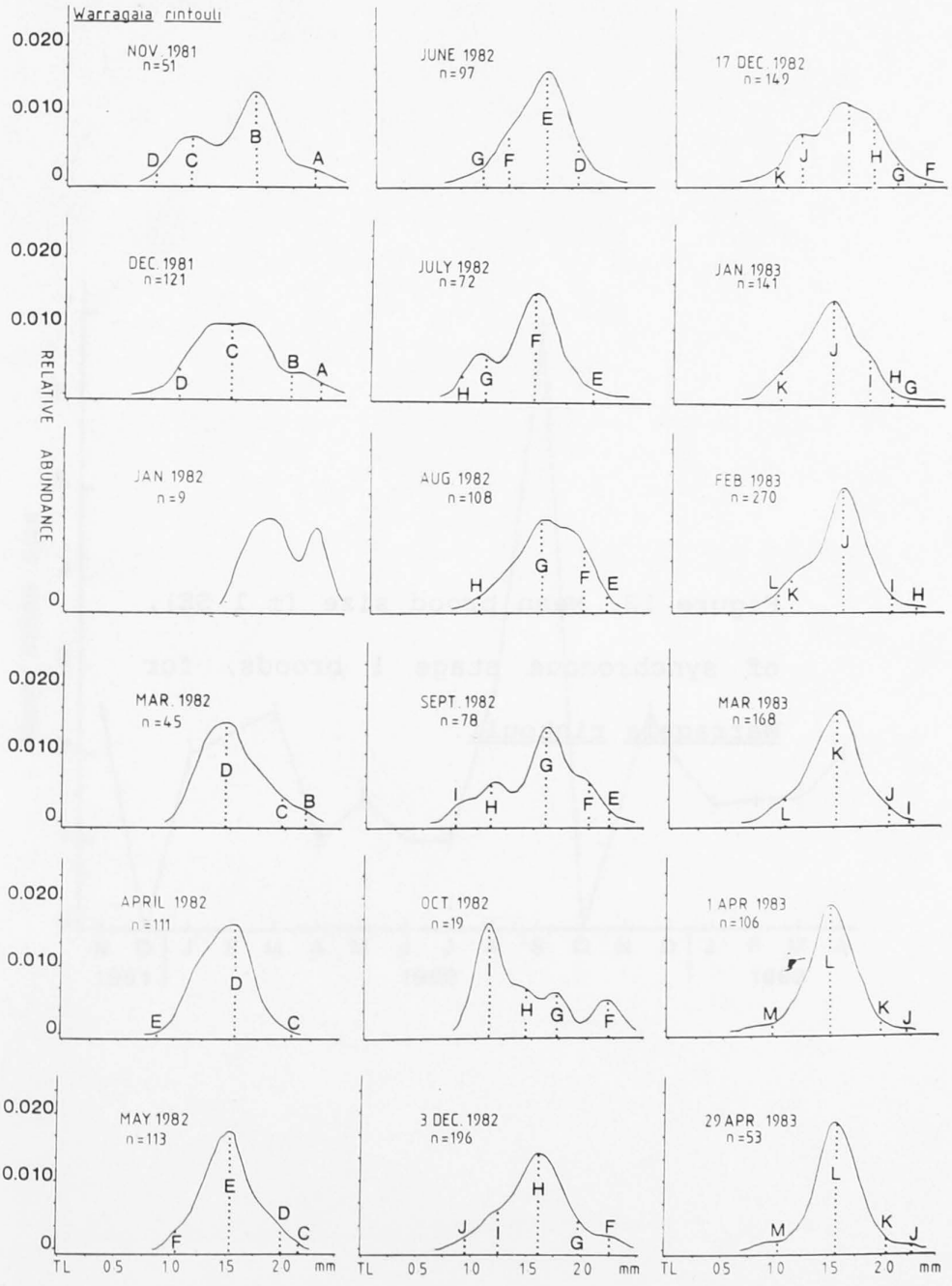

Brood Size
6
4
2
0
1.5
1.6
1.7
1.8
1.9
2.0
2.1
2.2
2.3
2.4
length of ovigerous female (mm)

Figure 11. Length-frequency data for Warragaia rintouli estimated by the non-parametric kernel density method. Dotted lines indicate the modal length of each cohort. The sample size in January and February 1982 was too small for cohort analysis. (Summer = Dec., Jan., Feb; autumn = Mar., Apr., May; winter = June, July, Aug; spring = Sep., Oct., Nov.)


Warragaia rintouli
NOV. 1981 n=51
JUNE 1982 n=97
17 DEC. 1982 n=149
DEC. 1981 n=121
JULY 1982 n=72
JAN 1983 n=141
JAN 1982 n=9
AUG 1982 n=108
FEB 1983 n=270
MAR 1982 n=45
SEPT 1982 n=78
MAR 1983 n=168
APRIL 1982 n=111
OCT 1982 n=19
1 APR 1983 n=106
MAY 1982 n=113
3 DEC. 1982 n=196
29 APR. 1983 n=53
RELATIVE ABUNDANCE
0.020
0.010
0
TL 0.5 1.0 1.5 2.0 mm

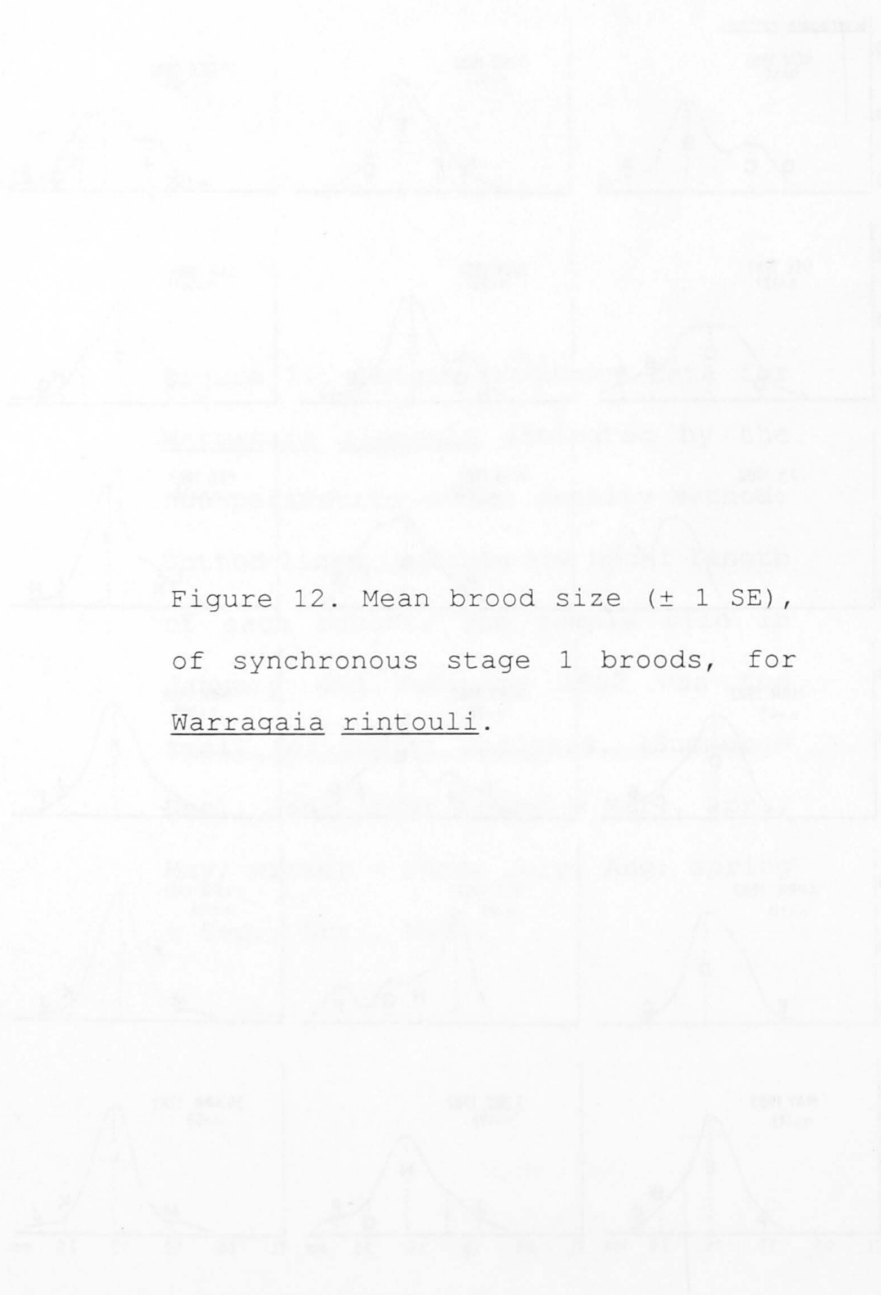
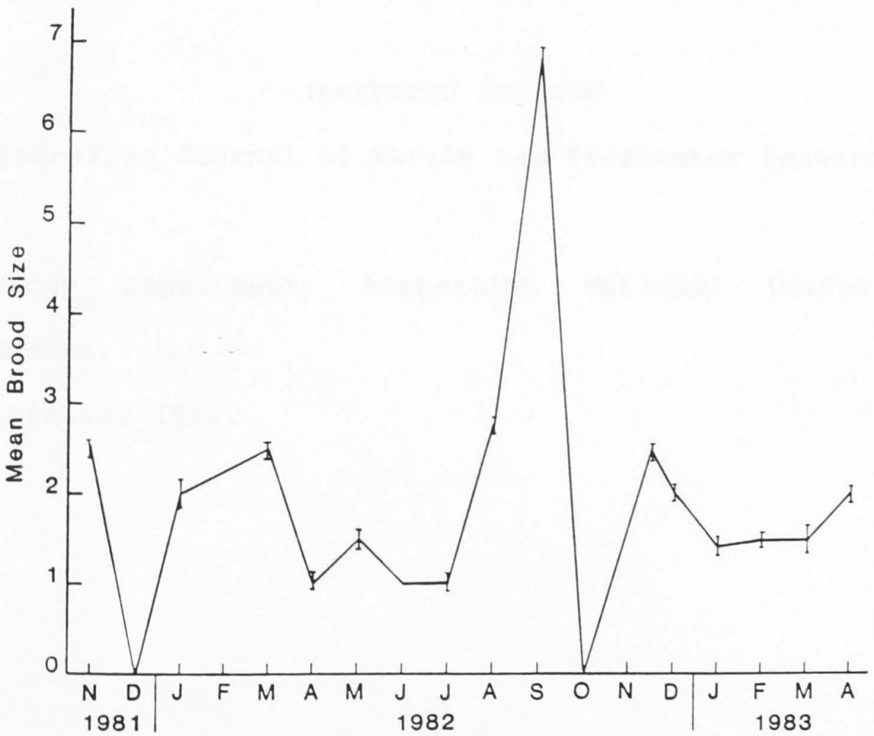


Figure 12. Mean brood size (± 1 SE), of synchronous stage 1 broods, for Warragaia rintouli.


Mean Brood Size
0
1
2
3
4
5
6
7
N D J F M A M J J A S O N D J F M A
1981
1982
1983

LIFE HISTORY AND POPULATION DYNAMICS OF AN EPIFAUNAL AMPHIPOD IN NEW SOUTH WALES.

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Canberra,
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ABSTRACT

The life history and population dynamics of the hyalid amphipod Hyale rubra (Thomson) were studied at Jervis Bay in New South Wales for eighteen months. Hyale rubra was an iteroparous species with seasonal reproduction and recruitment. Population density was greatest in summer. Generation time depended on the season of recruitment and brood size also varied seasonally. Brood size, egg size, sex ratios and generation times are reported. The reproductive strategy of H. rubra is shown to be similar to that of hyalids from the northern hemisphere.

INTRODUCTION

Hyalid amphipods are abundant in intertidal zones in both the Atlantic and the Pacific (Barnard, 1969; Gunnill, 1984). However, little is known of their life histories and most studies of these amphipods have been taxonomic (Iwasa, 1939; Hurley, 1957; Barnard, 1974 & 1979; Hiwatari & Kajihara, 1981; Hirayama 1985). Two hyalids whose life histories have been studied are *Hyale barbicornis* Hiwatari & Kajihara which lives amongst intertidal mussels in Japan (Hiwatari and Kajihara, 1984), and *H. nilssoni* (Rathke) an intertidal species which is found in algae on both sides of the Atlantic (Moore, 1983; McBane & Croker,1984).

There have been many studies of the life history of epifaunal amphipods in the family Gammaridae in the northern hemisphere (Nelson, 1980), and the data has been used to develop hypotheses about reproductive patterns of epifaunal amphipods (Van Dolah & Bird, 1980). The life histories of other epifaunal amphipod families have not been studied as comprehensively as the Gammaridae, and data from southern hemisphere epifaunal amphipods is not available. The aim of this study is to describe the life

history of Hyale rubra (Thomson), and to compare it with H. barbicornis and H. nilssoni and other epifaunal amphipods from the northern hemisphere. Hyale rubra is an algal dweller in intertidal and subtidal zones throughout the warm temperate regions of the North and South Pacific Ocean (Barnard, 1974).

This study forms part of a larger work which seeks to assess the hypothesis of Van Dolah & Bird (1980), which relates differential reproductive patterns between infaunal and epifaunal amphipods to predation risk. They proposed the hypothesis "that adult mortality is correlated positively with egg number and inversely with egg size". Future papers (Berents, thesis papers a, d) will describe the life history of two species of infaunal amphipods, and compare the risk of predation for infaunal and epifaunal amphipods.

METHODS

The study was carried out at Jervis Bay (35°05'S 150°45'E) on the south coast of New South Wales, Australia (Fig. 1). Hyale rubra was sampled from the brown alga

Caulocystis uvifera (C. Agardh) Areschough in one metre of water at Plantation Point, a relatively sheltered, shale headland.

Sampling Methods

Sampling was carried out each month from October 1981 until April 1983. The sampling programme was designed to yield at least 100 animals per month and was quantitative to allow estimates of monthly population densities.

Sea surface temperatures were recorded daily by H.M.A.S. Creswell at Jervis Bay and these data were made available by the Australian Oceanographic Data Centre (Berents, thesis paper a).

Four random samples of C. uvifera were taken each month with the aid of a mask and snorkel. A whole plant of C. uvifera was covered with a 500 μm mesh bag and pulled from the substratum. In order to sample similar proportions of stem and fronds in each sample, a whole plant was taken for each sample and preserved in 10 % formalin. On return to the laboratory the alga was placed

in an elutriator (Fig. 2) and all amphipods remaining on the mesh bag were retained. The elutriator was made from a large plastic funnel with a 500 μm mesh across the neck of the funnel. A rubber stopper, with narrow bore glass tubing through a hole in the middle of the stopper, blocked the neck of the funnel. The glass tubing was connected to plastic hose which was clamped to a tap to provide water at variable pressure. The alga was placed in the funnel and water flow controlled such that the alga was gently swirled and the overflowing water directed into a plastic tube, through the side of the funnel into a 500 μm sieve. The amphipods were dislodged from the alga, floated off in the moving water, and collected in the sieve. The alga was inspected for any remaining animals. The amphipods were sorted under a binocular microscope for Hyale species. Hyale rubra was distinguished from its congener H. maroubrae by the form of the first gnathopod of the male. For females and juveniles, the shape of the locking spines on the third and fourth peraeopods was examined to discriminate H. rubra.

The volume of each algal sample was measured by the displacement of water in a measuring cylinder. The sample

was blotted dry before each measurement, the volume measured three times and the mean calculated .

Laboratory Procedures

Hyale rubra were measured using an eyepiece graticule in a binocular microscope. As with most gammarideans, hyalids have a curved body which makes it difficult to measure total length accurately. The head length and total length were measured for a series of specimens of Hyale rubra and found to have a significant correlation. Head length was then measured from the remaining samples and total length derived from the regression equation, TL = 9.066(HL)-0.580 ($r = 0.9889$, $n = 45$). Female volume was measured as described by Berents (thesis paper a).

Secondary sexual characters were used to determine sex in adults. Males were determined by the presence of penial papillae on the sternum between the seventh peraeopods, and females by the presence of oostegites. Amphipods lacking these secondary sexual characters were regarded as juveniles. Staining with chlorazol black in lactophenol assisted in sex determination.

All eggs were removed from the brood pouch of every ovigerous female and the stage of embryonic development noted using Fish's (1975) classification (Berents, thesis paper a). Eggs were measured as described in Berents (thesis paper 1982).

Analysis of Data

Cohort Analysis

Cohorts of newly-recruited juveniles were identified using a combination of monthly length-frequency data and data on reproductive activity and population structure. Length-frequency distributions were estimated using the non-parametric kernel density estimate (Silverman, 1981). This method evaded the major weaknesses of the two main alternatives: histogram analysis and Harding's (1949) method (Berents, thesis paper a). The mode of the length of the amphipods in each cohort was estimated each month. Growth rates and generation time for each cohort were then calculated.

Life History Traits

Recruitment, brood size and mortality, reproductive activity and reproductive effort were defined as for Berents (thesis paper a).

RESULTS

Reproductive Activity and Recruitment

Ovigerous females were absent from the population throughout the winter (Fig. 3). Peaks in reproductive activity occurred in summer and autumn, when more than 50 % of females were ovigerous. In the following year, reproductive activity was again high in January and April.

Eleven cohorts (A-K, Figs. 4 & 5) were traced from October 1981 to April 1983 (Table 1). Six of these (C-H) were traced for the life span of the cohort. There were up to five cohorts in the population simultaneously although during the winter, sample sizes were too small for cohort

analysis. The sequence of recruitment of cohorts was as follows.

Juveniles were recruited to the population throughout autumn and summer in successive cohorts. The first cohort recruited in the summer of 1982 was cohort E in January 1982 which was the offspring of cohorts B and C. The population at this time was dominated by cohort D which had not reached reproductive maturity. By the following month, February 1982, cohort D was mature and cohort F was recruited to the population. In March reproductive activity exceeded 50 % and cohort G, which was the offspring of summer cohort E, was recruited to the population.

There was no recruitment in April 1982, but more than 50 % of females were ovigerous and cohort H, the offspring of cohort F, was recruited to the population in May 1982. Throughout the winter there was no recruitment and the population was dominated by juveniles of autumn cohorts G and H which did not reach reproductive maturity until late winter and late spring respectively.

Summer recruitment commenced in December 1982 and 69% of the population comprised juveniles (cohort I). These were the offspring of the previous autumn cohorts G and H. In January 1983 reproductive activity was still high and cohort J, which was the offspring of autumn cohort H, was recruited to the population. Summer cohort I was not then reproductively mature. In March 1983, cohort K was recruited to the population, the offspring of summer cohorts J and I.

Population Density and Structure

Hyale rubra was most abundant in Caulocystis uvifera in mid-summer (Fig. 6). In both summers, the population was dominated by juveniles (Fig. 7) from the cohort recruited in early summer (cohort D in 1982 and cohort I in 1983). In 1982 population density decreased steadily from the January maximum and remained low throughout winter and spring. During the winter the population comprised a few large adults from summer cohorts E and F but was dominated by juveniles (more than 70 % of the population comprised juveniles) from the autumn cohorts G and H. By late spring the autumn cohorts had reached

maturity, and juveniles comprised less than 35% of the population. By December the mean population density had increased following the recruitment of summer cohort I. Population density continued to increase to the January maximum with the recruitment of cohort J.

In late summer and autumn 1983, population density did not exhibit the steady decrease as seen after January in 1982, and in mid-autumn, at the completion of sampling, the mean population density was similar to the summer maximum.

Size Range

The mean ~~size~~ length of hatchlings in the brood pouch was 0.96 mm (Table 2). Juveniles outside the brood pouch ranged from 0.69 - 3.05 mm although penial processes were first discernible on males from 2.32 mm and oostegal buds were first discernible on females from 2.14 mm. The smallest ovigerous female was 2.50 mm and females were ovigerous up to the maximum size recorded of 5.04 mm. The largest H. rubra recorded were males of 5.95 mm.

The mean volume of ovigerous females was 0.92×10^{-3} ml ($n = 41$, 1 SE = 0.170×10^{-3}).

Sex Ratio

The ratio of males to females in the population of H. rubra fluctuated from 0.5 - 1.8 (Fig. 8) but over the entire sampling period the ratio was 1:1. At the end of winter there were more females than males in the sample, however by the time of peak reproductive activity in summer the ratio was 1:1.

Embryonic Development

Embryonic development followed the same pattern as described by Fish (1975) (see Berents, thesis paper a). For stage 2 eggs the caudal furrow could be distinguished and stage 3 eggs were defined by the presence of limb buds and the yolk was usually comma shaped. Stage 4 eggs were distinguished by segmentation of the body and the articles of the appendages. A pigmented eye was usually distinguishable at stage 4. Stage 5 embryos appeared fully

developed but were contained within the egg membrane. At stage 6, hatchlings occupied the brood pouch.

Brood Size and Brood Mortality

Brood size varied from one to 17 eggs with a mean of 5.5 (1 SE = 0.47, n = 68). There was a significant linear correlation between brood size and the length of ovigerous females, $y = 49.72x - 17.13$, ($r = 0.7030$, $n = 67$, $P < 0.01$) (Fig. 9).

Eggs within a brood did not all show synchronous development. Eighteen percent of broods comprised embryos at two successive stages of development.

The mean brood size of a brood of stage 1 eggs was 5.5 and the mean brood size of a brood of stage 5 eggs was 2.0 (1 SE = 0.5, n = 3) (Table 3). This difference in brood size was not significant ($t = 1.547$, $df = 69$).

The monthly mean brood size varied throughout the sampling period, with the largest mean brood sizes in late spring and autumn (Fig. 10).

Egg Size and Brood Volume

The mean diameter of eggs increased by 29.4 % from stage 1 (0.34 mm) to stage 5 (0.44 mm) (Table 4). The greatest increase in diameter between successive stages occurred between stages 4 and 5. The mean volume of stage 1 eggs was 2.06 x 10-2 mm^3 (1 SE = 2.0 x 10^{-3}, n = 393), which gave a brood volume of 1.13 x 10^{-2} mm^3 (Table 5).

Longevity and Time to Female Maturity

Hyale rubra recruited in early summer completed their life cycle by the end of summer or early autumn with a ~~generation time~~ life span of 133 days (cohort I) (Table 6). Those cohorts recruited in late summer (cohorts E and F) reached reproductive maturity in autumn, in a mean time of 40 ± 5 days, and their offspring were the autumn recruits which survived the winter to reproduce the following summer.

The cohorts recruited in autumn (cohorts G and H) had the longest ~~generation time~~ life span of 345 ± 35 days, and took 170 ± 5 days to reach maturity.

DISCUSSION

Hyale rubra was an iteroparous amphipod with seasonal reproduction, and peaks in recruitment in summer and autumn. Reproductive activity ceased in winter. The life history of Hyale rubra had many similarities with H. barbicornis and H. nilssoni (Moore, 1977; McBane & Croker, 1984).

Longevity

Many species of gammarideans in temperate environments have a short-lived summer generation and a longer-lived winter generation (Mills, 1967; Dexter, 1971 ; Rees, 1975; Moore, 1981; Dexter, 1985; Fenwick, 1985; Dauvin, 1988).

The ~~generation time~~ life span of H. nilssoni was approximately one year, whereas the ~~generation times~~ life spans of H. barbicornis and H. rubra varied with the season of recruitment. Summer populations had the shortest ~~generation time~~ life span (less than two months for H. barbicornis and five months for H.

rubra) and the overwintering populations had the longest generation times (eight to nine months for H. barbicornis and approximately eleven months for H. rubra).

All four cohorts of H. rubra (E, F, G, H) which were present through the winter, showed a marked slowing of growth rates from late autumn to early spring. Winter temperatures have been shown to cause slower growth rates in Ampelisca vadorum Mills and A. abdita Mills (Mills, 1967). Slow winter growth rates for H. rubra could be a result of low temperatures or limited food supply. At Jervis Bay, the lowest mean temperatures occurred from June to September (Berents, thesis paper a) which corresponded with the period of slow growth. The feeding preferences of H. rubra were not known but other hyalids were selective algal grazers (Moore, 1977; McGrouther, 1983). The distribution of subtidal algae at Plantation Point, Jervis Bay, varied seasonally (May & Larkhum, 1981) so it is possible that food availability affected growth rates of H. rubra.

Population Dynamics

Population density was low for six months of the year and this was a result of seasonal reproductive activity. At the beginning of winter there were few adults in the population which was dominated by autumn recruits. There was no recruitment until the following summer when the over-wintering juveniles matured to produce recruits in summer.

Reproductive Activity

Reproduction in H. rubra was seasonal, with no reproductive activity in the winter. Seasonal reproduction with reproductive activity ceasing in the cooler months, has been reported for many gammarideans (Van Dolah et al., 1975; Gable & Croker, 1977; Kolding & Fenchel, 1979; Wildish, 1979; La France & Ruber, 1985; Leineweber, 1985; Moore & Francis, 1986). Hyale nilssoni had no reproductive activity in the winter (Moore, 1983; McBane & Croker, 1984) but H. barbicornis had ovigerous females in the population all year, although the number of mature females decreased in the winter.

All three hyalids had more than one recruitment of juveniles each year. Hyale barbicornis had recruitment peaks in spring, summer and autumn, H. rubra in summer and autumn, and H. nilssoni in spring, summer and autumn. In both H. rubra and H. barbicornis numbers declined in winter, and survival of the population depended on the survival of the autumn recruits to reproduce in spring or summer.

Iteroparity

The data suggest that H. rubra was iteroparous because there were ovigerous females in the population every month except June, July and August. Cohort F was reproductively mature throughout this time and had ovigerous females before and after that period. The mean size of ovigerous females increased from 3.59 mm in May to 4.68 mm in September which suggested that females in this cohort were iteroparous, and produced broods in autumn and spring but not throughout winter.

Life history models predict that iteroparity will be selected in variable environments where adult survival rates are higher than those for juveniles (Murphy, 1968; Bulmer, 1985). Age-specific mortality rates for H. rubra are not known and it is not possible to conclude whether iteroparity is a response to juvenile mortality. Hiwatari & Kajihara (1984) reported H. barbicornis to be iteroparous.

Brood Mortality

Brood mortality of up to 58.5% has been recorded for epifaunal amphipods (Moore, 1981) but many studies also report negligible or insignificant brood mortality (Moore, 1981; Sheader, 1983; Bregazzi, 1972; Fenwick, 1985). Brood mortality for H. rubra was insignificant despite a 63.6 % change in brood size. The sample size for broods of stage 5 eggs was small, and the insignificant result may have been because the type II error was large (Toft & Shea, 1983).

Brood mortality is caused by many factors and these were discussed by Berents (thesis paper a). Unfertilized eggs were found occasionally in H. rubra broods.

Sex Ratio

Reproductive potential may be increased in iteroparous species if there are more females than males, because males may be able to fertilize more than one female (Wildish, 1979; Moore, 1981). Gammarideans may have more females than males during the breeding season (Moore and Francis, 1986) or the number of females may dominate all year round (Morino, 1978). Hyale rubra females outnumbered males during the spring, when the small overwintering population reached maturity. Egg production would be increased by a sex ratio in favour of females at the time when the population density was low.

Egg Size and Brood Size

Van Dolah and Bird (1980) listed the egg sizes of ten epifaunal amphipods and Hyale rubra eggs had small eggs

compared with other epifaunal species. The egg sizes of other hyalids were not known.

Amphipod brood sizes were usually proportional to the size of the ovigerous female (Sameoto, 1969; Bone, 1972; Strong, 1972; Hastings, 1981; Kolding & Fenchel, 1981; LaFrance & Ruber, 1985; Fredette & Diaz, 1986; Donn & Croker, 1986), so comparisons of brood size must consider female body size. Van Dolah & Bird (1980) compared brood sizes by calculating the brood size for standard size females (6 mm and 8 mm) using regression analysis. Hyale rubra did not reach 6 mm in length so the regression equation for brood size and female size of H. rubra could not be used in comparisons with the data of Van Dolah & Bird (1980). Nelson (1980) tabulated the mean brood sizes for 39 species of epifaunal gammarideans and found a range from 2.9 to 407. Hyalids were not included in Nelson's list, but Hyale barbicornis had a brood size from four to 23 eggs (Hiwatari & Kajihara, 1984) and H. nilssoni had a mean brood size of 10.5 to 31.4 (McBane & Croker, 1984). Compared with these species H. rubra had a small brood size.

The life history of *H. rubra* was strongly seasonal, and the key to the survival of the population was the summer recruitment following a winter period of slow growth with no reproductive activity and low population density. Both brood size and the proportion of females in the population, were at their greatest values in spring and this was an effective mechanism to maximize egg production. Three cohorts survived the winter with two juvenile cohorts dominating the small population. With the onset of spring the juveniles matured quickly to produce two fast growing summer cohorts. Temperature, photoperiod, and food supply have all been shown to influence the onset of reproduction in amphipods with seasonal reproduction (De March, 1977; Steele et al., 1977; Williams, 1978; Moore, 1983; Williams, 1985; Moore & Francis, 1986; Steele & Steele, 1986). The spring peak in recruitment for *H. nilssoni* in New Hampshire corresponded with warmer water temperatures (McBane & Croker, 1984).

Although *H. rubra* was a subtidal species and the Japanese species *H. barbicornis* was an intertidal dweller, both species faced a critical period through the winter and early spring. Although *H. barbicornis* maintained

reproductive activity throughout winter, population density was low and the number of females decreased, which resulted in the production of large numbers of eggs in the following spring. In summer H. barbicornis sought refuge from predators amongst mussels and was able to maintain high densities (Hiwatari & Kajihara, 1984).

This pattern of seasonal changes in reproductive traits, to cope with critical periods, may be found to be a widespread phenomena among the hyalids.

ACKNOWLEDGEMENTS

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Table 1. Modal head length of each cohort (mm) for Hyale rubra. During the winter sample sizes were too small for cohort analysis. (Summer = Dec., Jan., Feb; autumn = Mar., Apr., May; winter = Jun., Jul., Aug; spring = Sep., Oct., Nov.)

	Cohort										
Date	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**
Oct 1981	0.58	0.38									
Nov 1981											
Dec 1981	0.60	0.53	0.38	0.26							
Jan 1982	0.65	0.57	0.50	0.29	0.14						
Feb 1982		0.65	0.54	0.37	0.22	0.14					
Mar 1982			0.61	0.55	0.40	0.22	0.14				
Apr 1982			0.65	0.57	0.52	0.41	0.25				
May 1982				0.63	0.57	0.49	0.28	0.17			
Jun 1982											
Jul 1982											
Aug 1982											
Sep 1982					0.65	0.55	0.35	0.22			
Oct 1982						0.59	0.43	0.27			
Nov 1982						0.63	0.51	0.40			
Dec 1982						0.65	0.53	0.41	0.23		
Jan 1983							0.58	0.47	0.31	0.18	
Feb 1983							0.62	0.56	0.38	0.24	
Mar 1983							0.65	0.60	0.51	0.34	0.17
1 Apr 1983								0.67	0.54	0.43	0.29
29 Apr 1983									0.68	0.58	0.31

Table 2. Total length of Hyale rubra at different stages of maturity.

	Size range (mm)	Mean	1 SE (mm)	n
Hatchlings in brood pouch	0.51 - 1.78	0.96	0.01	27
Juveniles	0.69 - 3.05	1.87	0.01	944
Females	2.14 - 5.04	2.87	0.02	300
Males	2.32 - 5.95	3.59	0.01	448
Ovigerous females	2.50 - 5.04	3.65	0.09	194

Table 3. Mean brood size (number of eggs) at each stage of embryonic development (synchronous broods only) for Hyale rubra.

	Stage of Embryonic Development							
	1	2	3	4	5	6	Brood mortality %	Sig.
Hyale rubra	5.49	5.30	5.10	3.80	2.00	2.08	63.6	NS
n	68	7	34	9	2	12		

Table 4. Mean diameter (mm) of eggs at each stage of embryonic development for Hyale rubra.

	Stage of embryonic development 1	2	3	4	5
Hyale rubra	0.34	0.33	0.34	0.36	0.44
n	374	104	269	79	14
1 SE	0.001	0.003	0.002	0.005	0.015

Table 5. Brood volume and reproductive effort for Hyale rubra.

	Mean egg volume ± 1 SE (mm^3)	Mean brood size (number of eggs)	Brood volume (mm^3)	Reproductive effort %
Hyale rubra	0.0206	5.5	0.1131	12.3
1 SE	0.002	0.47		

Table 6. Seasonal life history patterns of Hyale rubra.

Recruitment	Female reproductive maturity	Mean time to ♀ maturity ± 1SE (days)	Death	Generation time ± 1 SE (days)	Cohort
early summer	summer	49 n=1	autumn	133 n=1	I
late summer	autumn	40 ± 5 n=2	spring/ summer	267 ± 32 n=2	E & F
autumn	spring	170 ± 5 n=2	summer	345 ± 35 n=2	G & H

LEGENDS FOR FIGURES

Figure 1. Location of study site at Jervis Bay, New South Wales.

Figure 2. Elutriator used for removing amphipods from algal samples.

Figure 3. Mean reproductive activity (the percentage of females that were ovigerous) and mean percentage of juveniles of Hyale rubra. Vertical bars indicate 1 SE. The replicates were combined for the first sample so standard error was not calculated.

Figure 4. Length-frequency data for Hyale rubra estimated by the non-parametric kernel density method. Dotted lines indicate the modal head length of each cohort. The sample size was too small in winter for cohort analysis. (Summer = Dec., Jan., Feb; autumn = Mar., Apr., May; winter = June, July, Aug; spring = Sep., Oct., Nov.)

Figure 5. Modal head length of cohorts of Hyale rubra. The size range of reproductive females is indicated.

Figure 6. Mean population density (± 1 SE) of Hyale rubra.

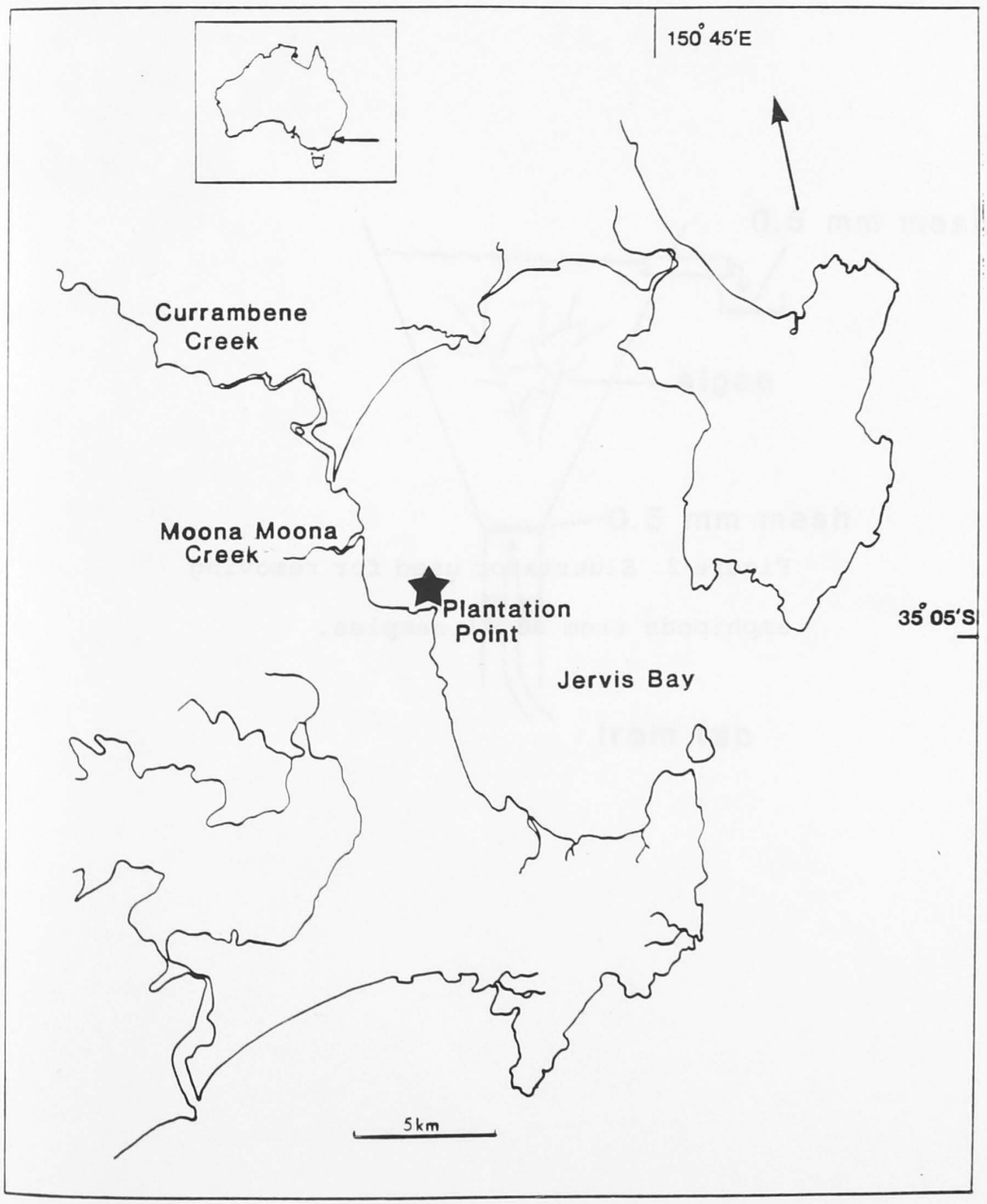
Figure 7. The percentage of males, females and juveniles in monthly samples of Hyale rubra.

Figure 8. The ratio of females and males of Hyale rubra.

Figure 9. Brood size (number of eggs) and head length of ovigerous females of Hyale rubra showing significant linear regression (y = 49.72x - 17.13).

Figure 10. Mean brood size (± 1 SE), of synchronous stage 1 broods, for Hyale rubra.

Figure 1. Location of study site at Jervis Bay, New South Wales.()


150° 45'E
Currambene Creek
Moona Moona Creek
Plantation Point
35° 05'S
Jervis Bay
5km

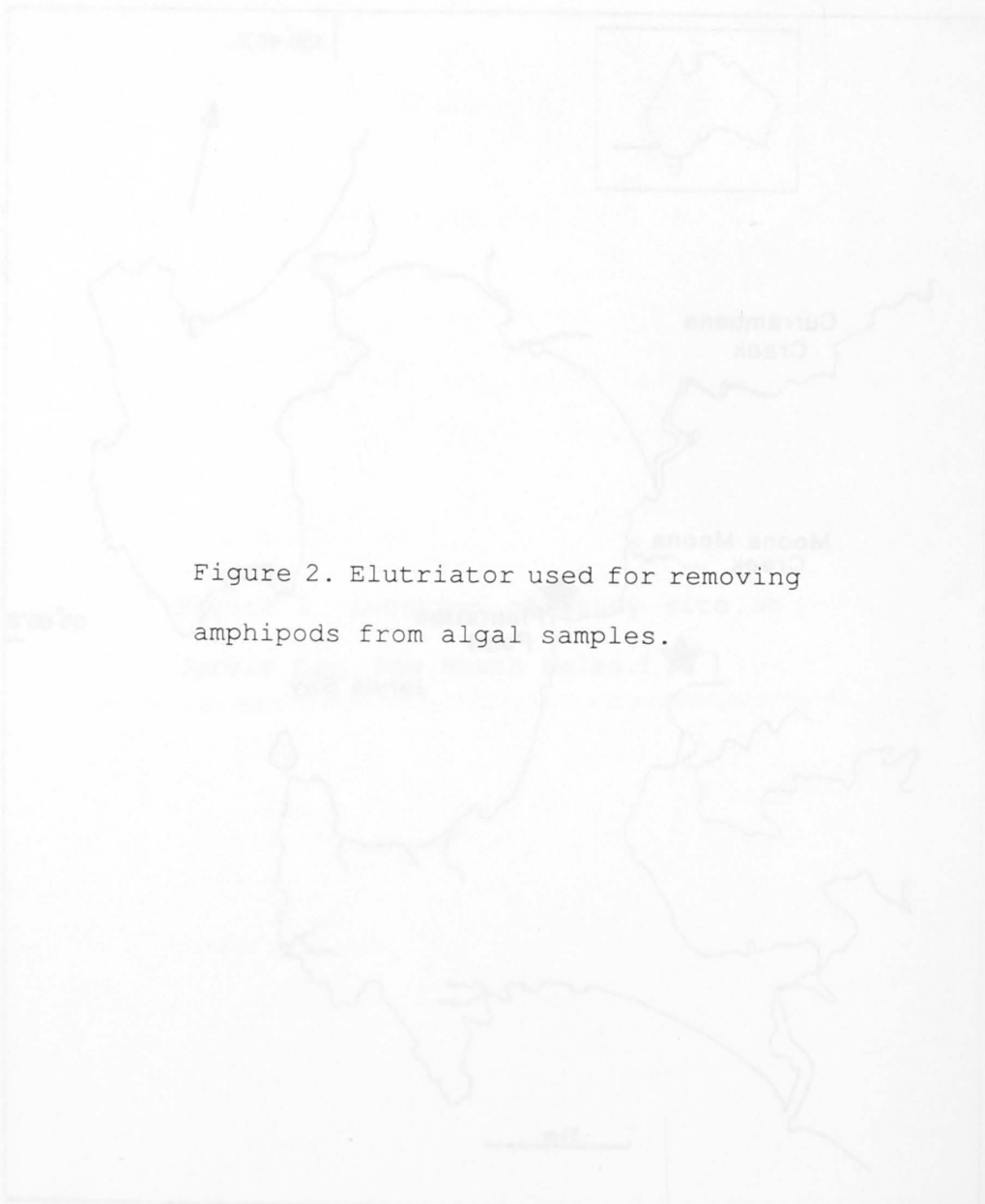
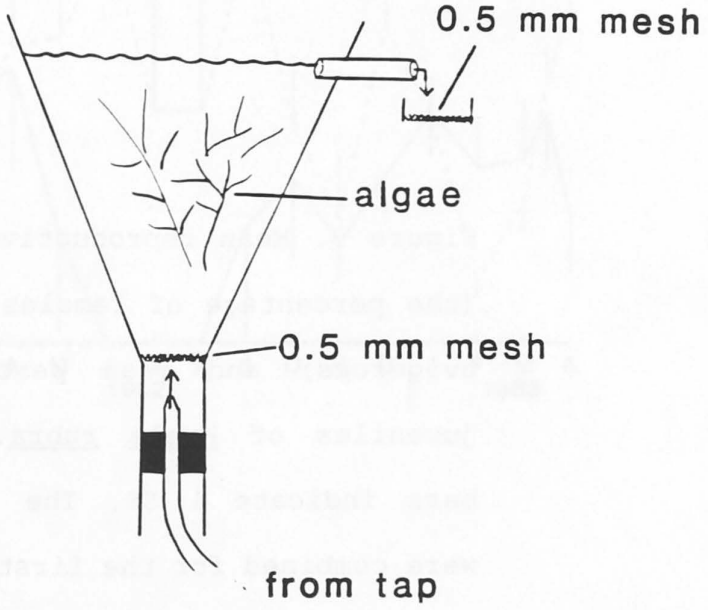


Figure 2. Elutriator used for removing amphipods from algal samples.


0.5 mm mesh
algae
0.5 mm mesh
from tap

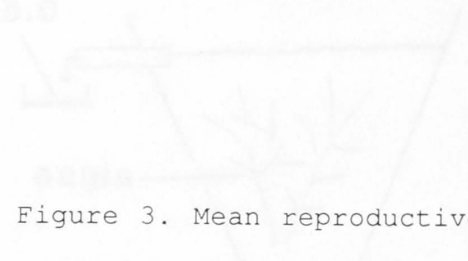


Figure 3. Mean reproductive activity (the percentage of females that were ovigerous) and mean percentage of juveniles of Hyale rubra. Vertical bars indicate 1 SE. The replicates were combined for the first sample so standard error was not calculated.

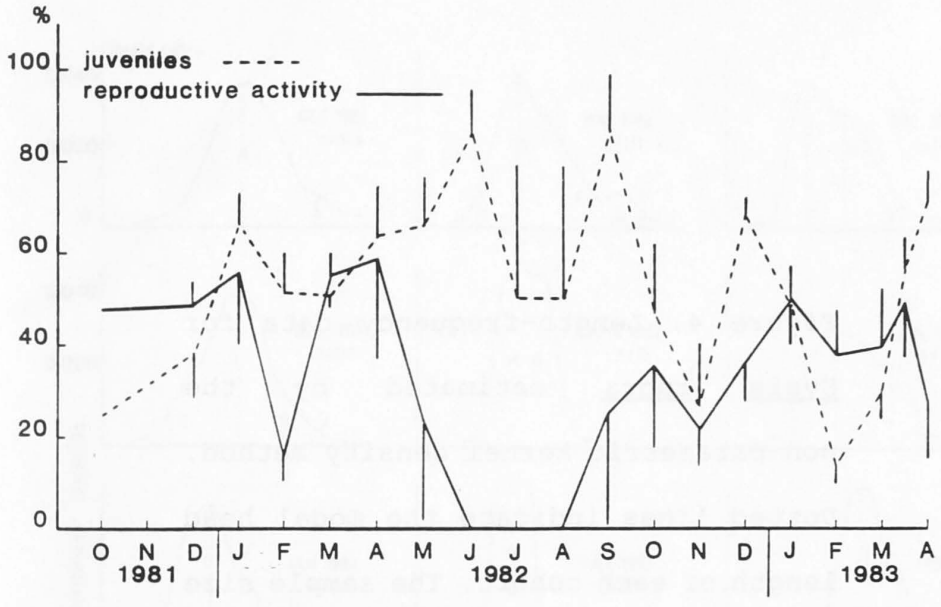

%
100
80
60
40
20
0
juveniles
reproductive activity
O N D J F M A M J J A S O N D J F M A
1981
1982
1983

Figure 4. Length-frequency data for Hyale rubra estimated by the non-parametric kernel density method. Dotted lines indicate the modal head length of each cohort. The sample size was too small in winter for cohort analysis. (Summer = Dec., Jan., Feb; autumn = Mar., Apr., May; winter = June, July, Aug; spring = Sep., Oct., Nov.)

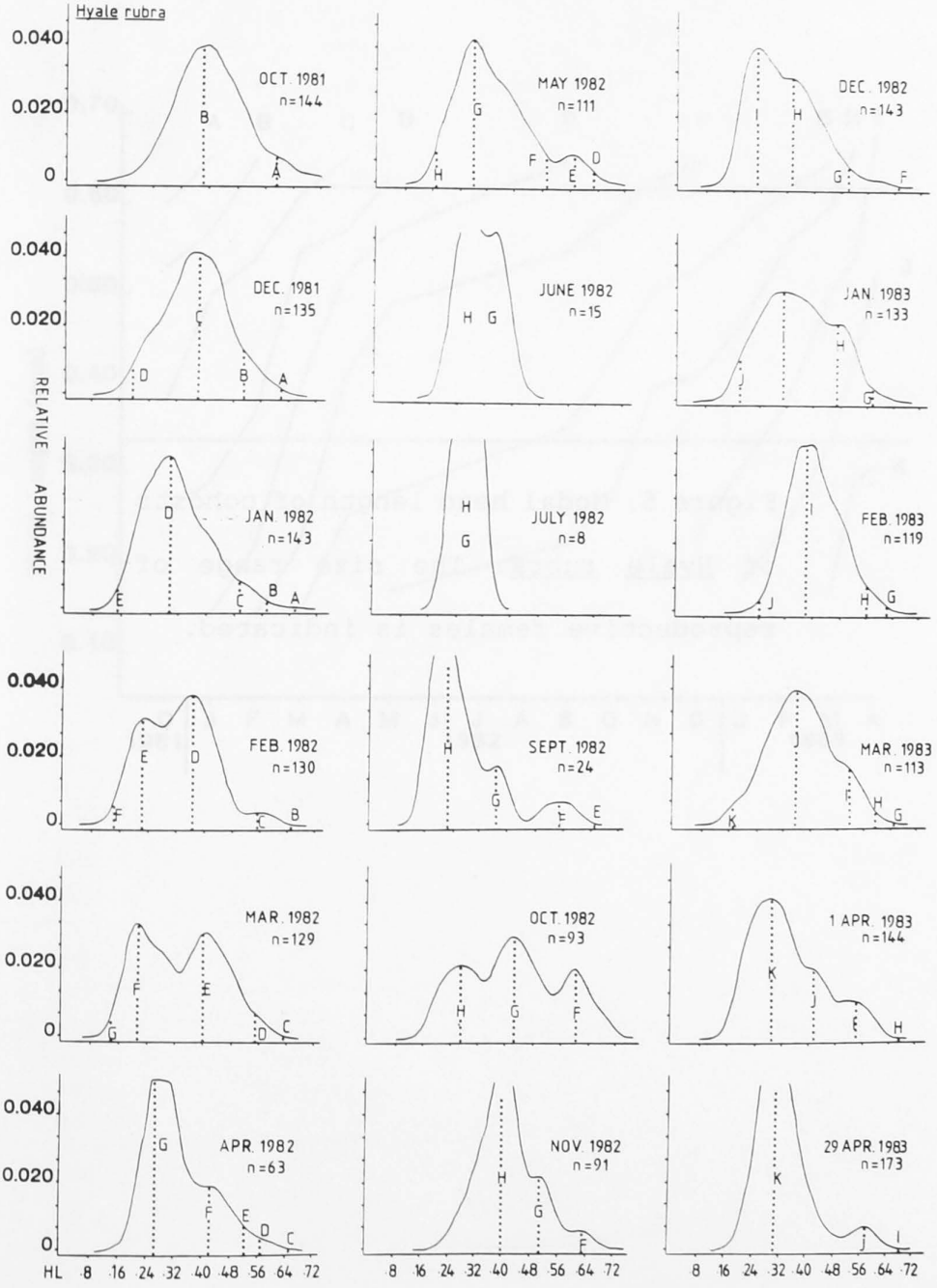
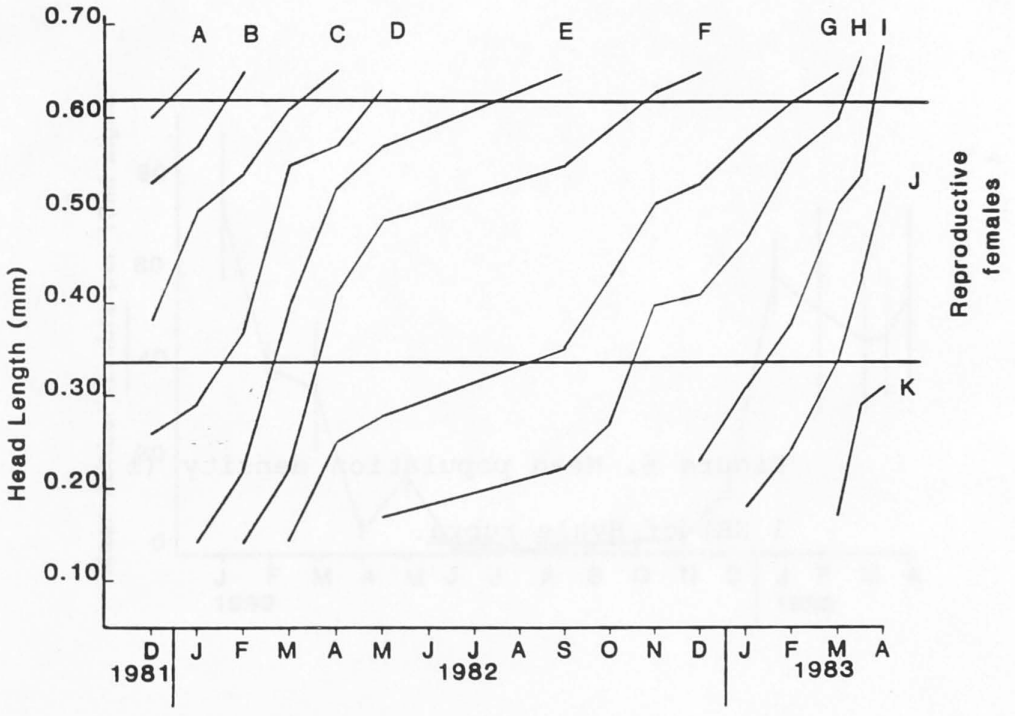

Hyale rubra
RELATIVE ABUNDANCE
HL
OCT. 1981 n=144
MAY 1982 n=111
DEC. 1982 n=143
DEC. 1981 n=135
JUNE 1982 n=15
JAN. 1983 n=133
JAN. 1982 n=143
JULY 1982 n=8
FEB. 1983 n=119
FEB. 1982 n=130
SEPT. 1982 n=24
MAR. 1983 n=113
MAR. 1982 n=129
OCT. 1982 n=93
1 APR. 1983 n=144
APR. 1982 n=63
NOV. 1982 n=91
29 APR. 1983 n=173
0.040
0.020
0
8 16 24 32 40 48 56 64 72

Figure 5. Modal head length of cohorts of Hyale rubra. The size range of reproductive females is indicated.


0.70
0.60
0.50
0.40
0.30
0.20
0.10
Head Length (mm)
A
B
C
D
E
F
G
H
I
J
K
Reproductive females
D
1981
J
F
M
A
M
J
J
A
S
O
N
D
1982
J
F
M
A
1983

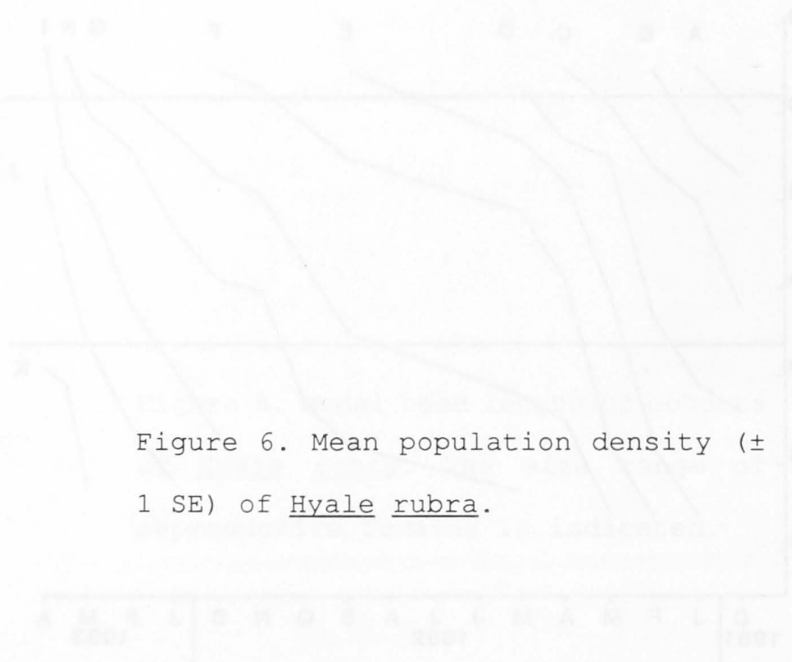


Figure 6. Mean population density (± 1 SE) of Hyale rubra.

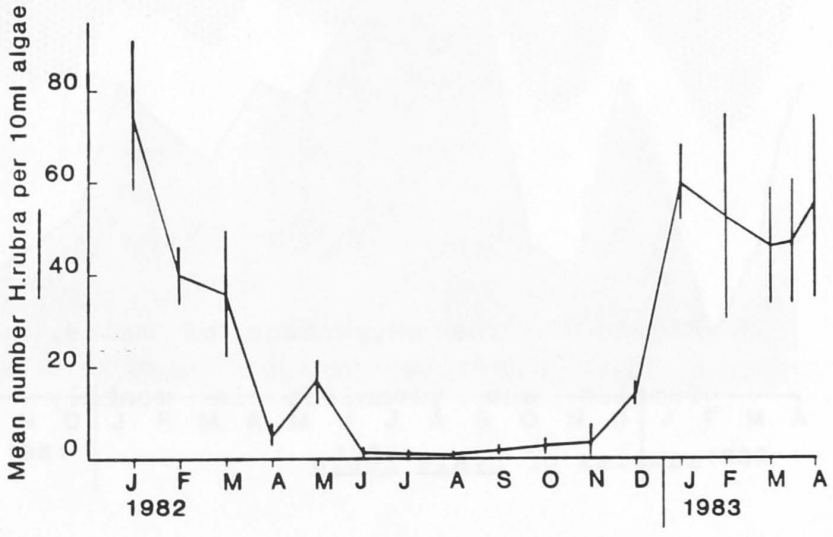
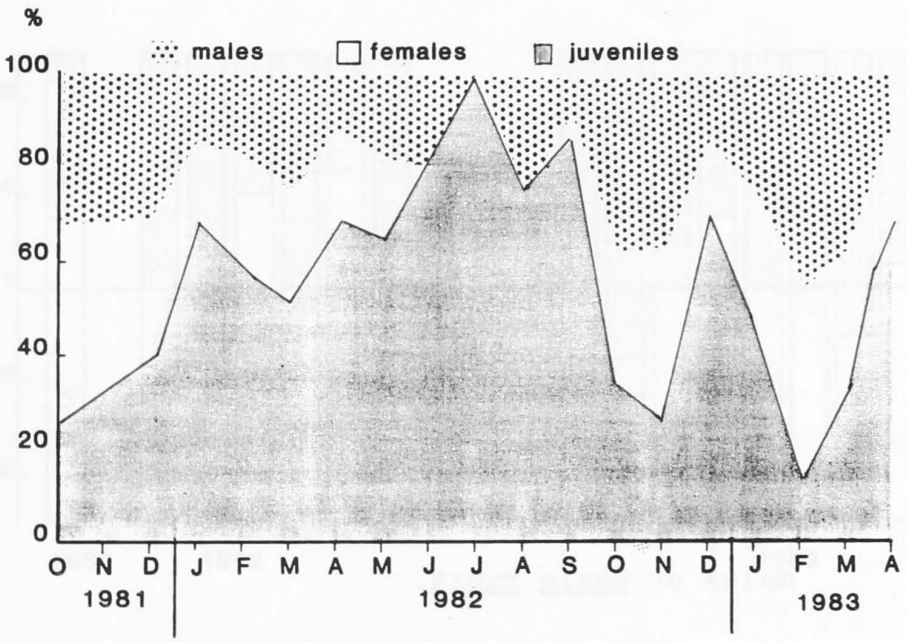

Mean number H.rubra per 10ml algae
80
60
40
20
0
J F M A M J J A S O N D J F M A
1982
1983

Figure 7. The percentage of males, females and juveniles in monthly samples of Hyale rubra.


%
males
females
juveniles
100
80
60
40
20
0
O N D J F M A M J J A S O N D J F M A
1981
1982
1983

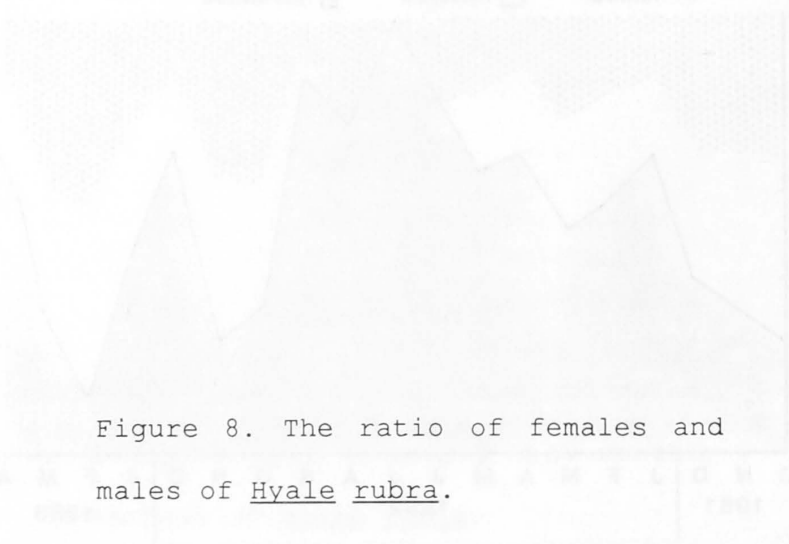


Figure 8. The ratio of females and males of Hyale rubra.

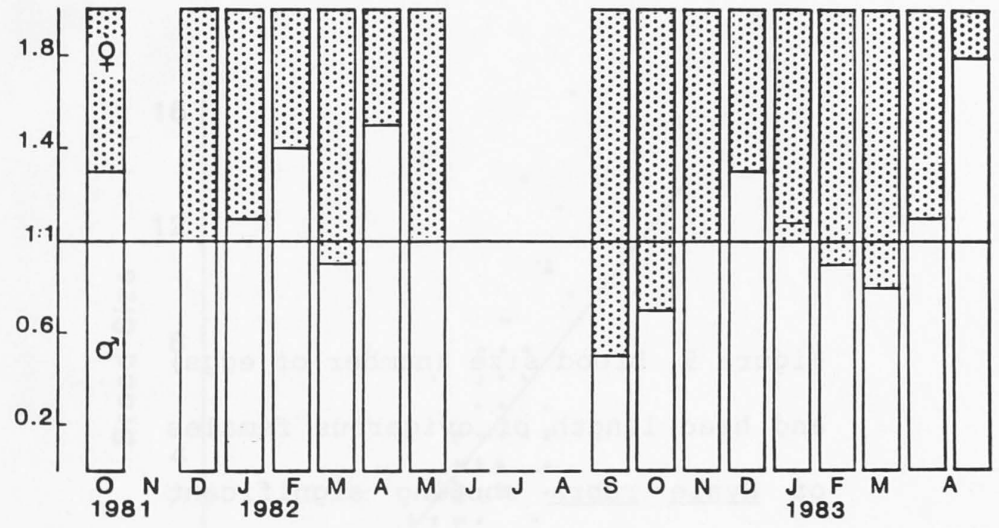

1.8
1.4
1:1
0.6
0.2
♀
♂
O N D J F M A M J J A S O N D J F M A
1981
1982
1983

Figure 9. Brood size (number of eggs) and head length of ovigerous females of Hyale rubra showing significant linear regression ($y = 49.72x - 17.13$).

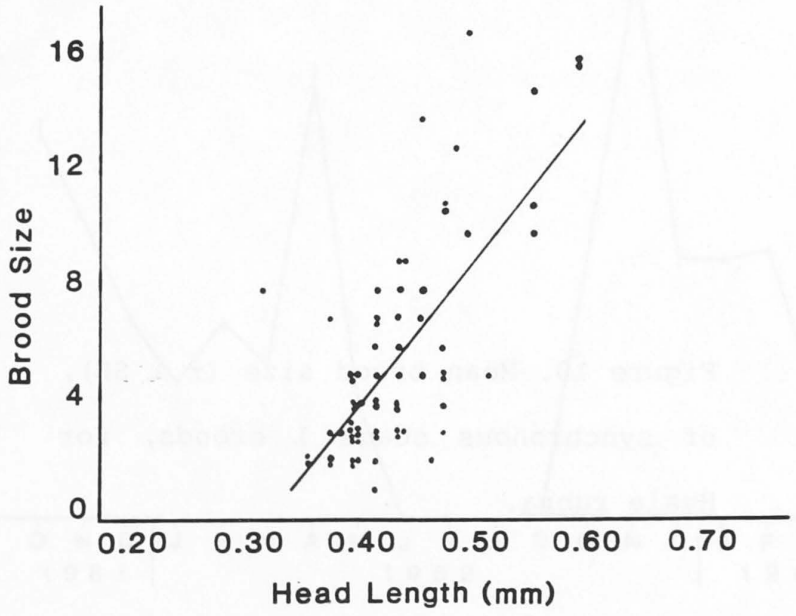
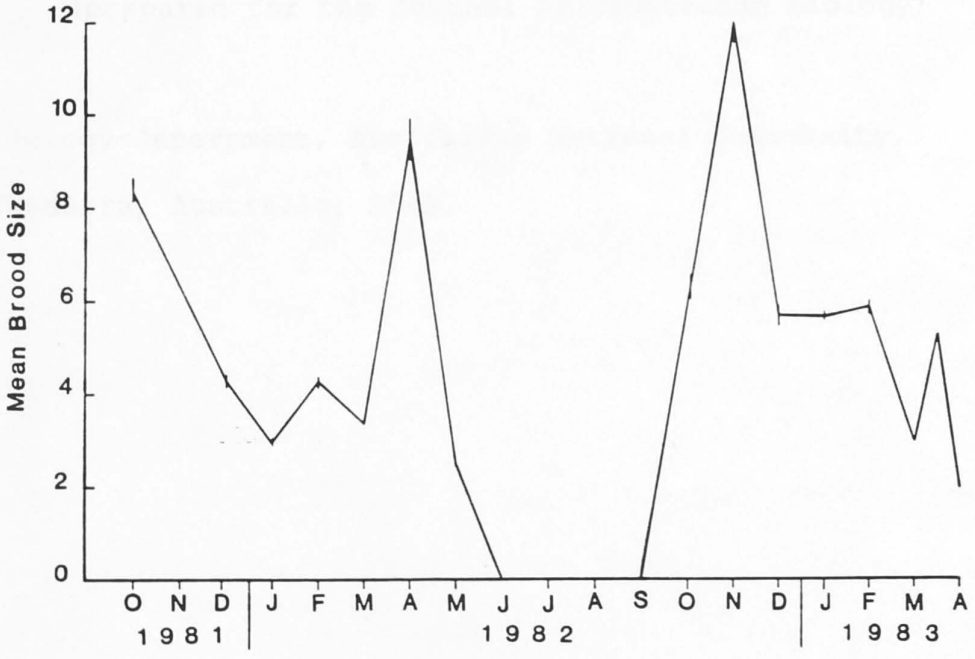

16
12
8
4
0
Brood Size
0.20
0.30
0.40
0.50
0.60
0.70
Head Length (mm)

Figure 10. Mean brood size (± 1 SE), of synchronous stage 1 broods, for *Hyale rubra*.


Mean Brood Size
12
10
8
6
4
2
0
O N D J F M A M J J A S O N D J F M A
1981
1982
1983

LIFE HISTORY AND POPULATION DYNAMICS OF THE COMMENSAL AMPHIPOD *LEUCOTHOE COMMENSALIS* HASWELL.

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(prepared for the Journal of Crustacean Biology)

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Canberra, Australia, 2061.

ABSTRACT

The life history and population dynamics of Leucothoe commensalis Haswell (Amphipoda, Leucothoidae) was studied at Jervis Bay, New South Wales for nineteen months. Leucothoe commensalis is a commensal of the ascidian Herdmania momus (Savigny) and an infection rate of 100 % was found. The number of L. commensalis found in the host varied from one to 204, and there was no seasonal pattern of abundance. Ovigerous females were found all year round and fecundity was high. Juveniles dominated the population in the host and there was usually only one mature female per host. The reproductive strategy reported for Leucothoe commensalis is new to amphipod biology and a model is proposed to explain the observations.

Chapter 4 - *Leucothoe commensalis*

INTRODUCTION

Amphipods live in association with many invertebrates. Associations of amphipods have been recorded with forams (Gooday, 1984), sponges (Hirayama & Kikuchi, 1980; Biernbaum, 1981; Lowry & Stoddart, 1983; Vader, 1984a & b, 1985), anemones (Vader, 1970b; Vader & Lonning 1973), hydroids (Lowry & Stoddart, 1983); medusae (Vader, 1972b), gorgonaceans (Lowry, 1984), brachiopods (Vader, 1970a), bryozoans (Lowry & Stoddart, 1983), polychaetes (Haines and Maurer, 1980), echinoderms (Vader, 1978), molluscs (Vader, 1972a; Underwood and Verstegen, 1988), crustacea (Taylor,1979; Steele et al., 1986; Thomas and Cairns, 1984), and tunicates (Harant, 1931; Thomas, 1979; Thomas & Taylor,1981; Lowry & Stoddart, 1983; Vader, 1984b).

Despite numerous records of these associations, the biology and life history of amphipod associations are poorly understood. Many published studies describe new species or document the occurrence of species which live in association with other animals, but few discuss the biology of the association (Vader, 1984b).

Chapter 4 - *Leucothoe commensalis*

The aim of this study is to describe the life history of *Leucothoe commensalis* Haswell, a commensal of the ascidian *Herdmania momus* (Savigny). *Leucothoe* is a widespread genus in the family Leucothoidae which is commensal in sponges and ascidians (Barnard, 1974). *Leucothoe commensalis* is found around the Australian coastline (Barnard, 1974) as a commensal in sponges (pers.obs.) and in the branchial chamber of ascidians (Barnard, 1974). He also reported *L. commensalis* as free living, but cast some doubt on the validity of this observation by stating that it was by "inference or negative evidence".*Herdmania momus* is a large solitary ascidian in the family Pyuridae, with a widespread tropical distribution which extends to southern Australia and southern Africa (Kott, 1985).

Vader (1983) reviewed the literature and summarized the available information about amphipod- sea anemone associations. He proposed four types of associations to describe the relationships between amphipods and their host anemones: protection only, ectocommensalism, endocommensalism, and micropredation. These categories may

also be applied to amphipod associations with other hosts.

Commensalism is an association between two species where the commensal derives shelter and is nourished by the host, but is not metabolically dependent on the host (Cheng, 1967). Leucothoids are filter feeders which are able to utilize the current generated by the ascidian to supply food (Thomas, pers. comm. 1989), so it is appropriate to consider them to be endocommensals.

METHODS

The study was carried out in Jervis Bay, southern New South Wales, Australia (35°05'S 150°45'E). The study site was a rocky reef with a dense cover of the laminarian Ecklonia radiata (C. Agardh) J. Agardh in four metres of water off Moona Moona Creek. Leucothoe commensalis was sampled in the ascidian H. momus which occurred in large numbers on rocky substratum (Fig.1).

Monthly sampling was carried out from October 1981 to March 1983, with preliminary sampling in August 1981.

Ten ascidians were collected randomly each month using scuba. A transect was run from the anchor of the boat in a random direction, and the first ten ascidians encountered along the transect were collected. A 500 μm mesh bag was placed over the ascidian and it was prised from the substratum. On return to the laboratory the ascidian was removed from the bag and the inside of the bag inspected for amphipods. The circumference of each ascidian was measured using a tape measure and each ascidian was opened using a scalpel. The ascidian was then laid flat in a dish and commensal amphipods were flushed from the branchial basket using seawater and a few drops of formalin. Each ascidian was inspected to check that all commensals had been removed. Five ascidians each month were selected randomly from the total sample of ten, and the total population of L. commensalis from each of the five ascidians was measured and sexed. A length frequency histogram was plotted for the population of L. commensalis in each ascidian. Each month, frequency distributions were estimated using the non-parametric kernel density estimate (Silverman, 1981) for the total number of L. commensalis

from the sub-sample of five ascidians. The presence of other commensals was noted.

For the remaining five ascidians, the total number of L. commensalis was counted, but only females were measured and the development of oostegites noted.

Laminarian holdfasts were sampled to establish whether L. commensalis could live outside H. momus.

The mean abundance of L. commensalis was calculated each month for the total sample of ten ascidians, and a one-way analysis of variance was used to test the null hypothesis that there was no significant difference between the abundance of commensals each month. Cochran's test was used to test for homogeneity of variance.

Reproductive activity was defined as the percentage of ascidians sampled which contained ovigerous females. All ovigerous L. commensalis were measured, and all the eggs or hatchlings in the brood pouch were counted. Ten eggs or hatchlings were selected at random and classified according to their stage of development.

Sex was determined for males by the presence of penial papillae on the sternum between the seventh peraeopods, and for females by the presence of oostegites. In order to determine sex for animals which lacked secondary sexual characters, histological sections were made of the gonads. The development of the brood pouch was classified by three stages:

Stage 1: oostegal buds, the oostegite barely discernible;

Stage 2: oostegites at full length but lacking lateral setae;

Stage 3: ostegites with lateral setae.

Females with stage 3 oostegites were considered to be reproductively mature.

It was difficult to measure the total length of L. commensalis because the body was curved. The head length and total length were measured for 117 specimens and found to have a significant correlation ($r = 0.9281$, $P < 0.01$). Head length was then measured for the remaining samples and total length derived from the regression equation, TL

= 10.85(HL) - 0.56. The mean volume of ovigerous females was measured as described by Berents (thesis paper a).

Fish's (1975) classification system for the embryonic development of Bathyporeia pilosa Lindström and B. pelagica (Bate) was used as the basis for defining the embryonic development of L. commensalis (Berents, thesis paper a).

Eggs and hatchlings were measured as described by Berents (thesis paper a).

In order to measure growth rates of the ascidian H. momus, seven H. momus were marked in situ and their circumference measured each month for six months.

Some pilot laboratory work was attempted with the aim of carrying out manipulations such as adding an extra mature female to a host with a resident pair, or observations of L. commensalis behaviour. It was not difficult to maintain H. momus in aquaria, but it proved impossible to manipulate or observe L. commensalis. Many methods were tried to dislodge the resident commensals,

both in situ and in the laboratory, but amphipods could only be collected by killing the host. Some questions may have been answered if observations could have been made inside the host, however it was not possible to pursue this aspect of the study.

RESULTS

Infection Rate

A total of 161 H. momus was examined during the 19 month study, and all were occupied by L. commensalis. Leucothoe commensalis was also found in laminarian holdfasts at the study site.

Six other commensal amphipod species were also found in H. momus (Tables 1 & 2) and each of these was also found in laminarian holdfasts. Notodelphyid copepods were also sometimes present in H. momus.

Abundance

The number of L. commensalis living inside one ascidian ranged from one to 204 with a mean of 52.4 (n=161, SE=3.6). Monthly changes in the abundance of L. commensalis in H. momus were not significant ($F_{18,142} = 0.78$, $P > 0.05$). On all sampling occasions, the variation in the numbers of commensals between different hosts was extremely high (Fig. 2).

There was no correlation between the number of L. commensalis living in the ascidian and the size of the ascidian ($r = 0.0360$, $n = 141$).

Reproductive Activity

Ovigerous females were found in H. momus every month of the year. There were none in November 1981 but in November 1982, reproductive activity was 33.3 %. Fifty percent or more of the ascidians sampled contained ovigerous females in summer 1981-2 and spring 1982, but this pattern was not observed in summer 1982-3 or spring

1981 (Fig. 3). Ovigerous females were not found outside H. momus.

Population Structure

The population of L. commensalis in most ascidians was dominated numerically by juveniles. Graphs of length frequency always showed one or two sharp peaks in abundance for amphipods less than 8.11 mm, with uniformly small numbers of larger amphipods (Fig. 4). In more than 75 % of all ascidians examined, the proportion of small L. commensalis (< 8.11 mm) exceeded 80 %. Of these small amphipods, approximately half were males and the other half lacked secondary sexual characters (females did not develop oostegal buds until at least 6.34 mm). Histological sections showed that the undefined L. commensalis were females.

The mean number of adults L. commensalis (> 8.11 mm) per ascidian was 2.9 (n = 94, SE = 0.4), and in 44.6 % of ascidians examined, one male and one female were the only adults present. The female was not always mature. The other ascidians had only females, or only males, or either

males or females may have been numerically dominant (Table 3). However, most ascidians (95.3 %) had no more than one reproductively mature female at a time. In those few cases (4.7 %) where two reproductively mature females were present, only one was ovigerous, and the other had oostegites at stage 3.

Males up to 9.42 mm and females up to 10.29 mm with stage 1 oostegites were found outside H. momus in laminarian holdfasts.

Brood Size

Brood size varied from 17 to 224 eggs with a mean of 99.3 (n = 51, SE = 7.7). There was no correlation between brood size and the size of ovigerous females (r = 0.0139, n = 51) nor between brood size and the size of the host ascidians (r = 0.0002, n = 49).

Size Range

Hatchlings reached up to 1.82 mm while inside the brood pouch. Of the small L. commensalis outside the brood

pouch, males developed penial processes when only 1.61 mm in length but females did not develop oostegites until they reached at least 6.34 mm. This suggested that males developed penial processes either before leaving the brood pouch or in one of the first moults after emergence. Females grew up to 19.40 mm and males grew up to 20.27 mm. The mean size of ovigerous females was 15.82 mm (n = 51, SE = 0.02) (Table 4).

The mean volume of ovigerous females was 0.0610 ml (n = 25, 1 SE = 0.015).

Egg Size and Brood Volume

The mean diameter of L. commensalis eggs increased by 22.2 % from stage 1 to stage 4 (Table 5). There were no eggs found at stage 5. Occasionally eggs were found which appeared not to have developed because there was no evidence of cell division. The mean volume of stage 1 eggs was 3.8 x 10-2 mm^3 and mean brood volume was 3.96 mm^3.

Size and Growth Rates of Herdmania momus

Herdmania momus greater than 300 mm in length showed very little increase in circumference over six months. However a specimen less than 300 mm in circumference increased in size by 24.4 % in six months (Fig. 5). There was no evidence of a successful larval settlement by H. momus in the two year period that the study site was visited. There was also no evidence of damaged or dead H. momus. The smallest H. momus sampled was 130 mm in circumference, and the mean circumference was 329.2 mm (n = 141, SE = 5.5).

DISCUSSION

Life History of Leucothoe commensalis

The life history of L. commensalis is unusual in that there was only one reproductively mature female in each ascidian at a time, despite the fact that many eggs and many juveniles were produced within the host. Reproductive activity was continuous and all available hosts were

occupied by L. commensalis. There was no seasonal pattern of abundance of L. commensalis.

It was difficult to analyse the life history of L. commensalis because the usual techniques based on cohort analysis (Moore, 1981; Hiwatari & Kajihara, 1984; Fenwick, 1985; Donn & Croker, 1986; Berents, thesis papers a & b) were not appropriate. Reproduction was continuous and there was no seasonal pattern of abundance or juvenile recruitment. Juveniles were numerically dominant at all times, with few adults in the population, so cohorts could not be traced. Furthermore, there was no synchrony between ascidians. On each sampling occasion there were ascidians with very few commensals, others with many commensals, some with ovigerous females, and others without ovigerous females. As a consequence, it was not possible to estimate generation times, or whether L. commensalis was semelparous or iteroparous.

Life History of Other Commensal Gammarideans

The life histories of other commensal amphipods whose biology has been studied are quite different. Onisimus

normani Sars lives in the gastrovascular cavity of sea anemones in the North Atlantic. Reproduction is seasonal, and the life cycle of O. normani takes two years. Ovigerous females have never been found in the host and are rarely found elsewhere. Onisimus normani enter the host as juveniles where they grow to adult size of 8-10 mm in 18 months, and then leave the host and disappear. Infection rates of up to 100 % have been recorded but the incidence of infection showed seasonal variation. Up to 20 commensals were found in a host (Vader, 1970b; 1983).

Orchomene recondita (Stasek) is also a commensal of sea anemones. Vader (1983) reported an infection rate of up to 80% and a mean of six commensals per host. Reproduction was seasonal and each female produced consecutive broods of 8-15 young with a life cycle of one year (Vader, 1983).

Stenothoe brevicornis (Sars) lives in association with a sea anemone and has continuous reproduction. The infection rate was 40-70 % with a mean of one to four amphipods per host.

Thomas (1979) described the occurrence of Anamixis hanseni Stebbing (as Leucothoides pottsi Shoemaker, see Thomas & Barnard, 1983) in the ascidian Ecteinascidea turbinata Herdman in Florida. Ovigerous females were observed within the transparent test of the tunicate and they carried 10-15 eggs. Anamixis hanseni filtered particulate matter from currents generated by the host and its own pleopods (Thomas & Taylor, 1981). Leucothoe commensalis produced more eggs, had a higher infection rate and had more amphipods per host than other commensal amphipods whose biology has been studied .

Life History of Other Ascidicolous Species

The biology of other commensals in ascidians has been studied by a number of workers but none of these species has a life history similar to L. commensalis. Egan (1984a & b) studied the reproductive cycles of a nemertean Gononemertes australiensis Gibson and a notodelyphid copepod Pachypygus australis Gotto, which were commensal in Pyura pachydermatina (Herdman), an ascidian in the same family as H. momus. Pyura pachydermatina was a winter breeding annual and the breeding cycles of the commensal

nemertean and copepod were correlated with that of the host. Reproductive activity of both commensals was continuous with a peak following the annual settlement of the host ascidian. Infection rates were from 90-100 %.

Gage (1966) also studied ascidicolous copepods which lived in a host with an annual settlement, and showed that their life cycles were correlated with that of their host.

Although the biology of a number of commensal species and their hosts has been studied, none shows much similarity with the life history of L. commensalis. Herdmania momus appears to be a much longer lived host species than those studied by Egan (1984a & b) and Gage (1966). There was no evidence of a successful settlement of H. momus during the two years that I visited the study site and their was also no evidence of mortality. Herdmania momus is a large and conspicuous animal with a thick tunic which is securely attached to the substratum. Empty or damaged tunics would be easily visible and difficult to dislodge. These observations are consistent with those of Svane & Lundalv (1982) and Svane (1983) in

a study of another pyurid ascidian, Pyura tessellata (Forbes) in Sweden. They found that individuals lived longer than the 12 year period of their study and that recruitment was at a rate of less than one individual per m^2 per year.

Fecundity

Prior to this work it was thought that commensal amphipods had low fecundity (Vader, 1983), however L. commensalis demonstrated that this is not always so. Few gammarideans have larger brood sizes than L. commensalis. Of the 65 species listed by Nelson (1980), only three had a larger brood size. Fecundity is a measure of the reproductive capacity of a female and includes egg production, generation time and the duration of reproductive activity. There is little known about the generation times and the duration of reproductive activity for most commensal and parasitic crustacea so discussion here is limited to brood size.

Parasitic copepods exhibit both low and high egg numbers and Gotto (1962) discussed the factors which

influenced these patterns. Gotto suggested that high egg number is found in copepods associated with either sparsely distributed, inaccessible hosts, or highly mobile hosts, or hosts which live in environments that made infestation difficult, such as the intertidal zone or high wave energy shores. Herdmania momus, however, was abundant, sessile and subtidal.

Hyperiidean amphipods are parasites of gelatinous zooplankton. Laval (1980) argued that Hyperiidean have larger brood sizes than gammaridean amphipods, including commensal gammarideans, because of the risks associated with finding a host in a pelagic environment. Hyperiideans achieve a large brood size by reducing egg size, a feat which is possible because hyperiidean hatchlings are not fully developed, and the host serves as a secondary brood pouch (Laval, 1980). The brood size of L. commensalis was within the same range as that of hyperiideans (Table 6).

In hyperiideans and copepods, large brood sizes are associated with a high risk in finding or infecting a host. In L. commensalis the risk was imposed by the lack of available hosts. Little is known of the life history or

settlement patterns of H. momus, but my observations suggested that settlement is either infrequent or at a very low level, such as with P. tessellata. All available hosts were occupied, and new hosts rarely become available. A large brood size is desirable to maximise the chances of offspring finding a host when one becomes available. Settlement by H. momus may be infrequent but on a large scale, in which case a large brood size would increase the number of hosts which may become infected with offspring. The usual disadvantage of having many small eggs is the low reproductive fitness of the hatchlings (Smith & Fretwell, 1974). This, however, is not a problem for a commensal living inside a host, because the host provides a safe environment for the newly hatched young.

Conclusions

The life history of L. commensalis is characterised by three features which are new to amphipod biology. The first is that there is only one mature female in the host at a time. Secondly, the population was dominated numerically by juveniles at all times and the most common

pattern was for only two to three adults to be present in a host. And finally, a large brood size has never been recorded for commensal gammarideans. Although this study was not able to provide a complete understanding of the life history of L. commensalis, a hypothesis can be proposed to explain the available data.

This hypothesis assumes that the young are offspring of the resident large mature female who either leaves the ascidian or dies after producing her brood or broods. One of the female offspring then develops to maturity first, and remains in the ascidian to become the mother of the next generation. By the time they reach about 8 mm in length, her siblings have left the ascidian. Females develop oostegal buds from 6.34 mm, so it is possible that none of the siblings start to develop oostegites while in the host, and that maturation of females is suppressed, perhaps by the female who matures first.

A similar situation occurs in cleaner wrasse, where the top female in a harem changes sex to become the dominant male (Robertson, 1972 & 1973). The male cleaner wrasse who dominates all the females in the harem is

derived from the top female, and the presence of the male suppresses the tendency of the females to change into males. It is possible that in L. commensalis only the top female becomes mature and remains in the ascidian to produce young.

The male who mates with the new mother may be promiscuous, and visit a number of hosts in search of females with whom to mate, or he may be a sibling who also remained in the host. If he is a sibling then inbreeding would result with no prospect of any exchange of genetic material. This, however, may not necessarily be a disadvantage for a commensal species. Price (1980) argued that parasites were advantaged by a slower rate of evolution through reduced variation, because a slower rate of genetic change was more likely to allow coevolution with their longer lived hosts.

What becomes of the young L. commensalis which do not reach adult size in the host? One possibility is that they leave the host in search of new hosts. Leucothoe commensalis were found outside the ascidian but reproductively mature females have only been found inside

H. momus. Some of the searchers may find another host, although at my study site H. momus was the dominant host and all of these were already occupied. The risks of predation on L. commensalis which leave the safety of the host are not known.

Although a male and female pair was the most common pattern in adults there were occasions where smaller males and immature females were also present. These may be other siblings which were not yet mature, or they may be searchers from another host. Perhaps the resident female or the resident pair defend their host from other mature L. commensalis, but allow immature animals to enter. If searchers were allowed to enter the host and eventually reproduce, this would preclude the idea of genetic continuity through the female line or through sibling parents.

Many of the unanswered questions about the life history of L. commensalis could be answered by experimental manipulation if appropriate techniques could be developed. Does the mature female defend her host from

other females? What happens if the adult pair are removed from the ascidian?

Although the life history of L. commensalis reveals patterns that are new to amphipod biology, there are parallels with parasites and other amphipods. Parasites have evolved patterns of reproduction such as parthenogenesis, hermaphroditism and asexual reproduction which enable an individual to maintain populations in a host (Rohde, 1982). Hermaphroditism has also been reported for commensal lysianassoid amphipods (Lowry & Stoddart, 1986).

The ascidian H. momus offers L. commensalis a safe, long term, habitat but limited opportunity for offspring to disperse. The unusual life history pattern described for L. commensalis provides a compromise between the risks of dispersal and the benefits of life in the host. Many eggs mean that L. commensalis is ready for dispersal but probably on most occasions there is high mortality. However, continuity of genetic material within the host may be guaranteed by one sibling who becomes the next

mother, or two siblings who become the next parents. Siblings have half their genes in common and Hamilton (1972) argues that, in the extreme case, a sibling could sacrifice its life, with no loss of reproductive fitness, if two of its siblings survive to reproduce. Once a female, or pair is ensconced in the host, the lineage is perhaps maintained by their offspring and then their offspring's offspring who remain in the ascidian and in their turn reproduce.

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Table 1. Percentage of Herdmania momus with Leucothoe commensalis and other commensal amphipods.

	%
L. commensalis only	43.3
L. commensalis with one other species	29.2
L. commensalis with two other species	17.7
L. commensalis with three other species	8.0
L. commensalis with four other species	1.8

Table 2. Mean number and percent occurence of each commensal species in Herdmania momus. The mean is calculated with n equal to the number of ascidians in which the commensal occured.

	Mean ± 1 S.E.	%
Leucothoe commensalis Haswell	52.4 ± 3.6	100.0
Paraleucothoe novaehollandiae (Haswell)	5.2 ± 1.3	25.7
Leucothoella gracilis (Haswell)	1.8 ± 3.6	11.5
Leucothoe assimilis Barnard	1.0 ± 0	1.8
Leucothoe n.sp.1	16.5 ± 4.2	36.3
Leucothoe n.sp.2	5.7 ± 3.0	5.3
Anamixis sp.	2.0 ± 0.5	2.7

Table 3. The distribution of adult Leucothoe commensalis in host ascidians Herdmania momus.

	Number of H.momus sampled	% of H.momus sampled	% of n with a mature female
One female & one male	42	44.6	65
One female only	13	13.8	77
More than one female (females only)	4	4.3	75
More males than females	14	14.9	70
More females than males	11	11.7	66
Equal numbers males & females (but more than a pair)	6	6.4	66
Males only	3	3.2	-
No adults	1	1.1	-

Table 4. Total length (mm) of Leucothoe commensalis at different stages of maturity.

	n	Mean	Range
Hatchlings in brood pouch	41	1.50	0.74 - 1.82
Females with stage 1 oostegites	71	8.34	6.34 - 11.16
Females with stage 1-2 oostegites	41	11.27	7.69 - 14.20
Females with stage 2 oostegites	34	13.44	9.42 - 15.06
Females with stage 3 oostegites	69	15.28	9.86 - 17.67
Ovigerous females	51	15.82	12.46 - 19.40
Males	128	4.89	1.61 - 20.27

Table 5. Egg size for Leucothoe commensalis at each stage of embryonic development.

	Stage of development				
	1	2	3	4	5
mean (mm)	0.42	0.47	0.49	0.54	
n	170	87	108	41	0
S.E.	0.004	0.012	0.005	0.008	

Table 6. Brood size of commensal gammarideans and parasitic hyperiideans.

	Brood Size	Reference
Commensal gammarideans		
Orchomene recondita	8-15	Vader, 1983
Anamixis hanseni	10-15	Thomas, 1979
Leucothoe commensalis	17-224	this work
Parasitic hyperiideans		
Parathemisto japonica	up to 200	Laval, 1980
P. pacifica	20-60	"
P. gaudichaudii	10-200	"
Hyperia galba	60-450	"
Lycaea pulex	up to 228	"
Vibilia armata	approx. 120	"
V. propinqua	approx. 120	"
V. jeangerardi	70	"
Lestrigonus schizogeneios	36	"
Hyperoche medusarum	48-94	"

LEGENDS FOR FIGURES

Figure 1. Location of study site (*) at Jervis Bay, NSW, Australia.

Figure 2. The abundance of Leucothoe commensalis in the ascidian Herdmania momus showing the mean number per host ± one standard error, and the range of values. Summer = December, January,February; autumn = March, April, May; winter = June, July, August; spring = September, October, November.

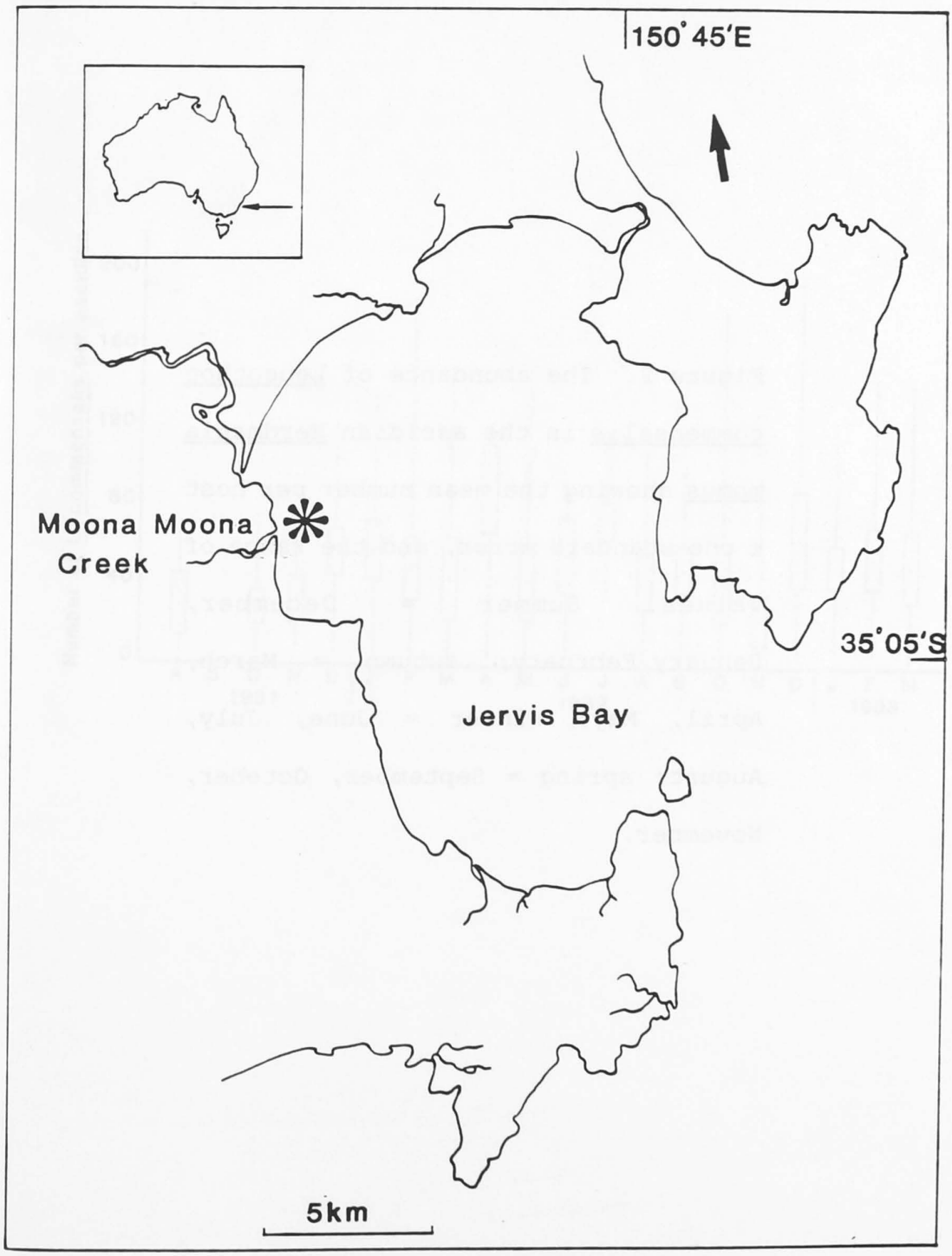
Figure 3. Reproductive activity (the percentage of ascidians containing an ovigerous female) of Leucothoe commensalis in a sample of ten ascidians Herdmania momus. (Summer = December, January, February; autumn = March, April, May; winter = June, July, August; spring = September, October, November)

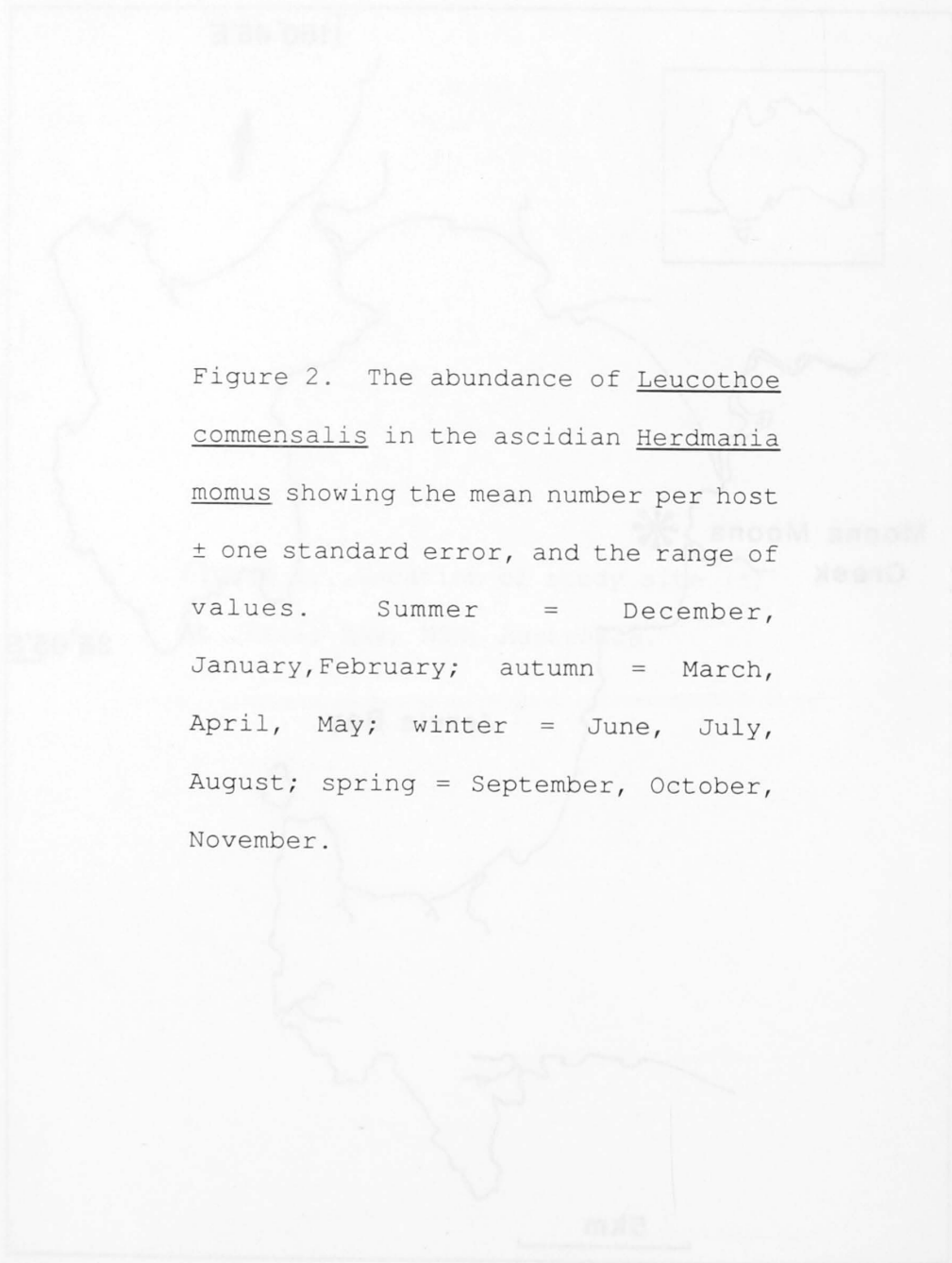
Figure 4. Size frequency distribution of Leucothoe commensalis found in five ascidians Herdmania momus sampled in summer (December, 1981, n=260), autumn (March, 1982, n=328), winter (August, 1982, n=199), and spring (October, 1982, n=116).

Figure 5. Size of seven ascidians Herdmania momus measured in situ.

Figure 1. Location of study site (*)

at Jervis Bay, NSW, Australia.


150°45'E
Moona Moona
Creek
35°05'S
Jervis Bay
5km



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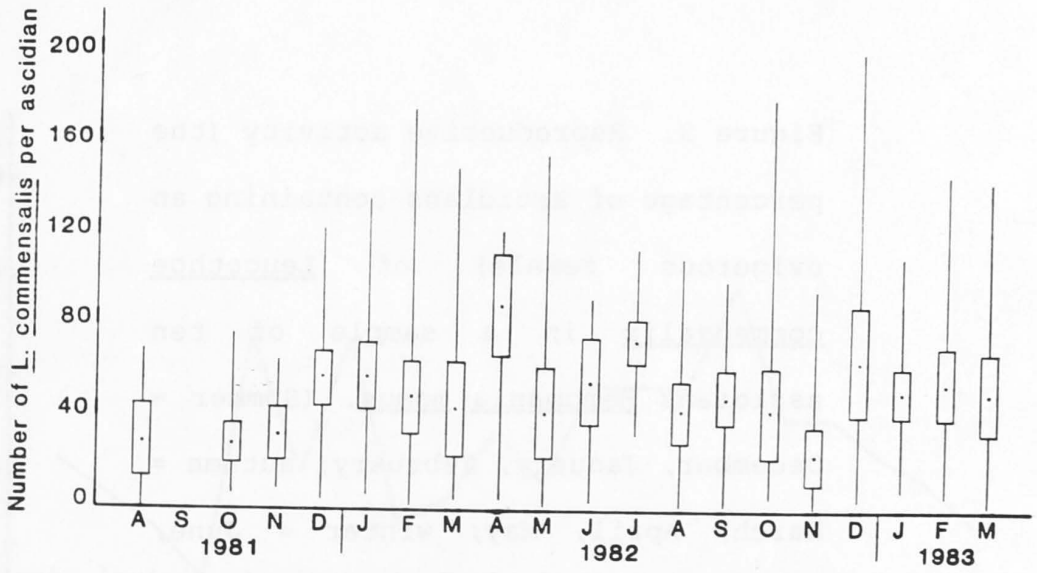

Number of L. commensalis per ascidian
200
160
120
80
40
0
A S O N D J F M A M J J A S O N D J F M
1981
1982
1983

Figure 3. Reproductive activity (the percentage of ascidians containing an ovigerous female) of Leucothoe commensalis in a sample of ten ascidians Herdmania momus. (Summer = December, January, February; autumn = March, April, May; winter = June, July, August; spring = September, October, November)

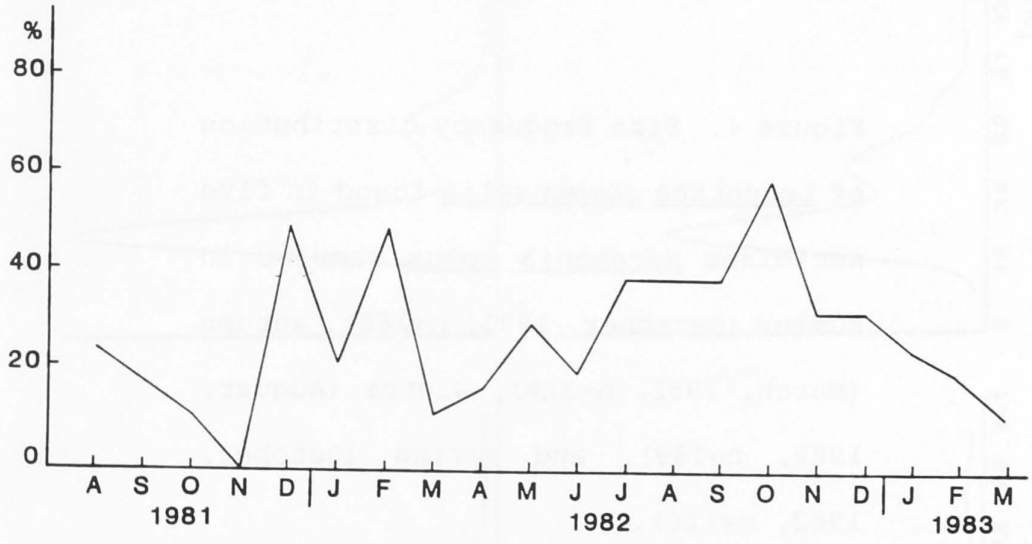

%
80
60
40
20
0
A S O N D J F M A M J J A S O N D J F M
1981
1982
1983

Figure 4. Size frequency distribution of Leucothoe commensalis found in five ascidians Herdmania momus sampled in summer (December, 1981, n=260), autumn (March, 1982, n=328), winter (August, 1982, n=199), and spring (October, 1982, n=116).

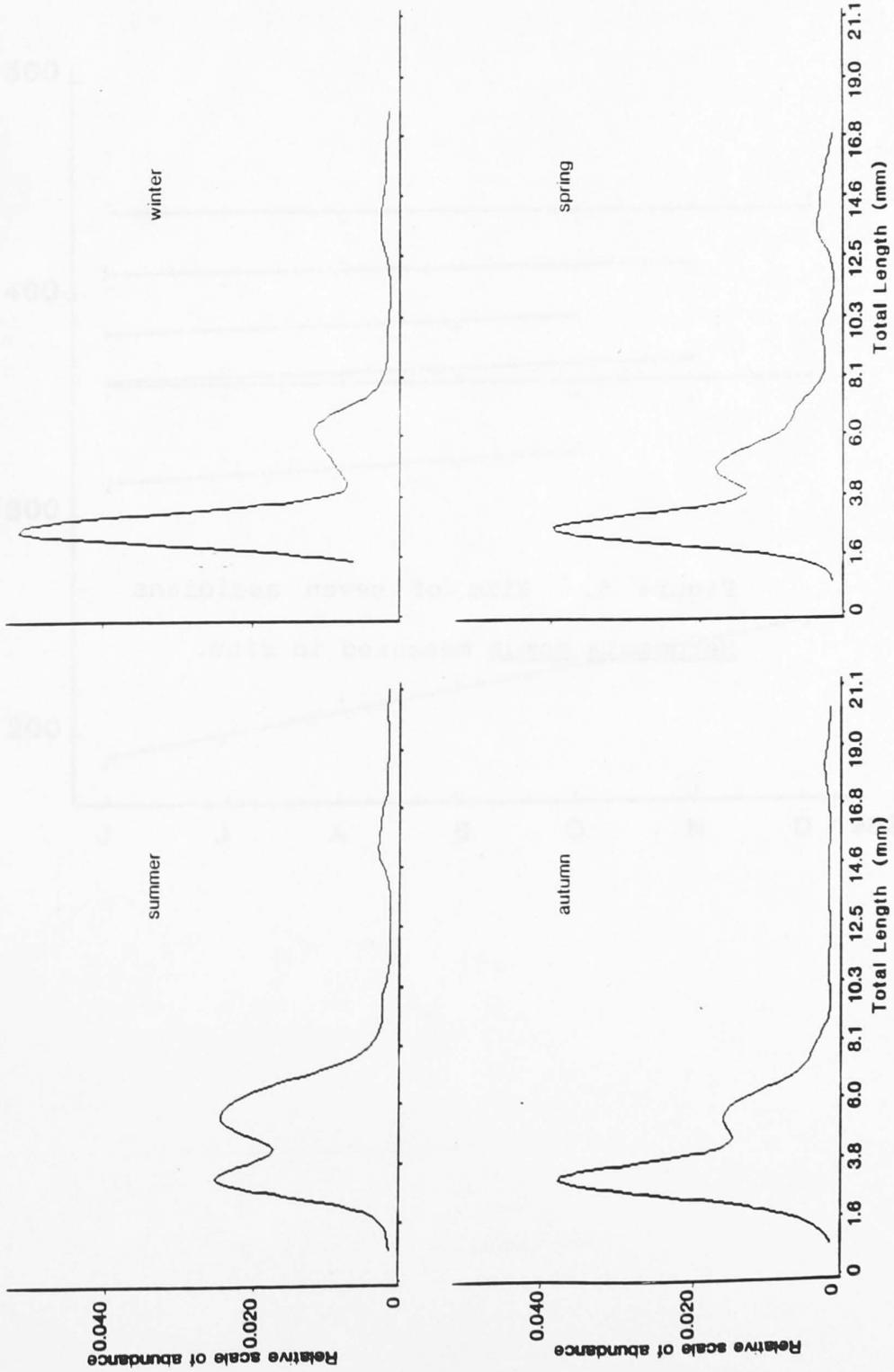
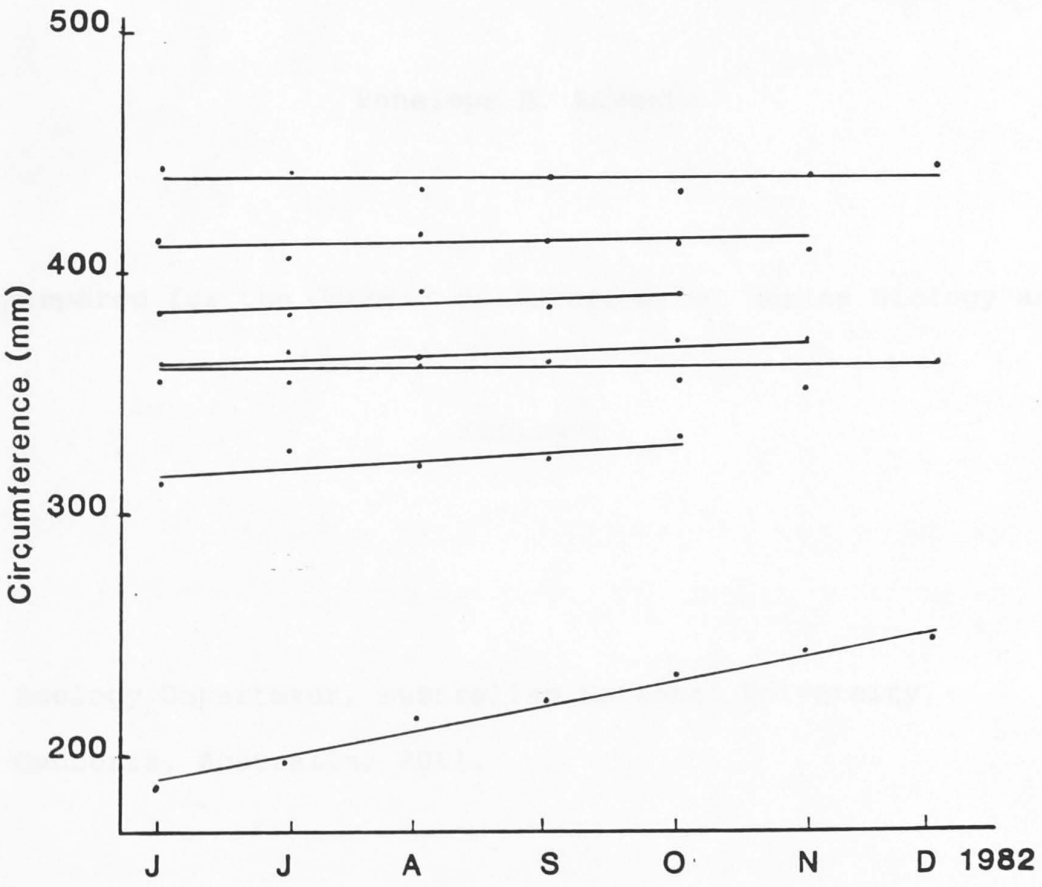

winter
spring
summer
autumn
Relative scale of abundance
0.040
0.020
0
0 1.6 3.8 6.0 8.1 10.3 12.5 14.6 16.8 19.0 21.1
Total Length (mm)

Figure 5. Size of seven ascidians *Herdmania momus* measured in situ.


500
400
300
200
Circumference (mm)
J
J
A
S
O
N
D
1982

DIFFERENTIAL EFFECTS OF PREDATION ON INFAUNAL AND EPIFAUNAL MARINE AMPHIPODS

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(prepared for the Journal of Experimental Marine Biology and Ecology)

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ABSTRACT

Field experiments were conducted at Jervis Bay, NSW to compare the effects of predation on epifaunal and infaunal amphipods. New experimental techniques were developed to undertake this work - mesh exclusion bags and scour plates. Mesh bags were used to exclude predators from Hyale rubra (Thomson) living on sublittoral brown algae. Cages were used to exclude predators from the burrowing amphipods Urouaustorius metunqi Fearn-Wannan and Warraqaia rintouli Berents. Scour plates were used to minimize cage induced changes to the sediment, and at one site sediment analyses of cages and controls revealed no changes in the substratum.

Examination of gut contents of fish collected at the study sites revealed several species which prey on U. metunqi, W. rintouli and H. rubra.

After a period of three weeks, no significant predation effect was detected for U. metunqi, however for H. rubra the exclusion of predators led to an increase in numbers. It was not possible to draw conclusions about the effect of predation on W. rintouli because the results of the experiment were confounded by artifacts.

INTRODUCTION

Predation has been implicated as an important factor in structuring marine communities in a number of habitats (Sih et al, 1985). On the intertidal rocky shore, fishes (Gibson, 1972; Coull & Wells, 1983) and invertebrates such as gastropods (Connell, 1961; Garrity & Levings, 1981), and starfishes (Paine, 1966) are important predators. In temperate subtidal reef habitats, many studies have shown that fishes prey on motile invertebrates, and predation has been considered to cause small invertebrates to aggregate around shelter (Choat, 1982).

In contrast, soft-sediment habitats have often been the subject of manipulative field experiments designed to examine the effects of predation. The use of exclosures and enclosures to examine the effect of predation on infauna is a well-established technique (Arntz, 1977; Reise, 1977; Virnstein, 1977; Reise,1978; Virnstein, 1979; Holland et al., 1980; Mahoney & Livingston, 1982; VanBlaricom, 1982; Kent & Day, 1983; Ambrose, 1984b; Quammen, 1984; Gee et al, 1985;). Although many workers

have used exclosures and enclosures in soft-sediments this technique is not without problems. Cages may cause changes to the environment which confound the results of the experiment, by modifying the sediment, attracting predators, or by changing patterns of recruitment or larval settlement (Virnstein, 1978; Dayton & Oliver, 1979; Hulberg & Oliver, 1980; Reise, 1985).

In a review of the reproductive patterns of gammaridean amphipods Van Dolah & Bird (1980) suggested that observed differences in egg size and number may be a function of different adult mortality risk in different environments. As a result of comparing reproductive patterns for infaunal and epifaunal amphipods they proposed that the observed difference in reproductive patterns may be attributed to the risk of predation in each habitat. However, data allowing the comparison of adult mortality risk and reproductive patterns for species at the same locality are not available.

The aim of this study is to compare the risk of predation for epifaunal and infaunal amphipods at one locality and to identify some of the predators involved.

The reproductive patterns of each species were also studied and reported elsewhere (Berents, thesis papers a & b). The epifaunal amphipod chosen for study was the hyalid Hyale rubra (Thomson) which lives in subtidal algae, and the infaunal species were the sand burrowing urohaustoriids Urouaustorius metungi Fearn-Wannan and Warragaia rintouli Berents. New techniques are described to (i) exclude predators from epifaunal algal dwellers and (ii) to minimize environmental changes caused by exclosures in soft-sediments.

METHODS

The experiments were carried out in Jervis Bay, southern N.S.W., Australia, (35°05'S 150°45'E), at a time of high amphipod densities (Berents, thesis papers a & b).

Infaunal Intertidal Experiment

The intertidal infaunal experiment was conducted at Site 1, on a tidal sandflat in the lower reaches of Currambene Creek which is the largest freshwater creek flowing into Jervis Bay (Figure 1). Monthly sampling of

the sandflat for U. metungi showed that the region of maximum density varied. Before setting up the cages, core samples were taken along a transect from MHW to MLW to determine the region of maximum density. The exclosures and controls were then placed randomly along a line parallel to the waters edge at a level where U. metungi was most abundant, 20 metres from the upper edge of the sandflat.

The experiment was a completely randomized design with three treatments (exclosure, control for exclosure effects, and control for predation effects). Each treatment was replicated three times and six random core samples were taken within each.

The 0.6 x 0.6 x 0.2 metre exclosures and controls were constructed from a welded frame covered with one mm fiberglass mesh (Figure 2). The controls for cage effects were exclosures without a mesh top. Exclosures and controls were anchored to the bottom by a guy rope from each corner and tied to a peg driven into the sand. Preliminary trials showed that the exclosures and controls caused scouring of sand from around the base of the

structures which allowed predators to enter the exclosure. To prevent scour, galvanized metal plates were placed on the surface of the sand around the outside of the exclosures and controls. The inner edge of the scour plate was bent to vertical so that it formed a lip inside the exclosure. The controls for predation effects were areas of sand 0.6 x 0.6 m.

The potential problems of caging experiments in soft sediments raised by Virnstein (1978), Dayton & Oliver (1979) and Hulberg & Oliver (1980), were given careful consideration. A number of types of exclosures and controls were tried in pilot studies before the final design was determined. Sediment scour at the edges and deposition of finer sand in the middle of the exclosures were obvious artifacts until scour plates were used. Scour is caused by turbulence from water currents being deflected by the fine mesh of the exclosure which acts as a barrier to water flow (P. Crapper, pers. comm.). The scour plate was designed to prevent the turbulence from picking up sand from outside the edge of the cage. During the course of the experiment the scour plates became partially covered

with sand and also helped to anchor the exclosures and controls.

The experiment was set up on 27th November 1983 and sampled three weeks later. The exclosures and controls were lifted from the sediment and six cores (of diameter 10.7 cm, depth 12 cm) were taken from within the area of each. Each core was washed through a 500 μm sieve and the amphipods removed, preserved in 70 % ethanol, and later counted under a binocular microscope. The means and variances for the number of U. metunqi per core were calculated for each treatment and the means were transformed to $\log_e$ to stabilize the variance. The null hypothesis that the mean density of U. metunqi was not significantly different between the treatments was tested using analysis of variance.

Sediment samples of approximately 90 gms each were taken from exclosures and controls at the completion of the experiment. The samples were dried, shaken through a nest of sieves (2000 μm, 850 μm, 600 μm, 425 μm, 250 μm, 106 μm, 53 μm), and the sediment remaining on each sieve weighed. The mean grain size (Folk & Ward, 1957), sorting

(Gray, 1981), skewness (Miller, 1967) and percent silt-clay were calculated for each.

Infaunal Subtidal Experiment

The infaunal subtidal predation experiment was conducted at Site 2 off Moona Moona Creek in eight metres depth of water (Figure 1). The exclosures and controls were identical to those described previously for the intertidal site. The only difference was that the exclosures and controls were tied to heavy objects in the sand in addition to guy ropes which were secured to pegs.

The experiment was a completely randomized design with three treatments (exclosure, control for exclosure effects, and control for predation effects). Each treatment was replicated three times. The treatments were placed randomly on the sandy bottom.

The experiment was set up on 27th November 1983 and sampled three weeks later. It was necessary to scrub the mesh of the exclosures and controls daily after the eighteenth day to remove fouling.

The exclosures and controls were lifted from the bottom and four quadrats (0.2 x 0.2 m) sampled from within each by an airlift. The samples were retained in 500 μm mesh sample bags and preserved in 70 % ethanol. The animals were later removed from the sediment by swirling in water (Berents, thesis paper a) and counted under a binocular microscope. The means and variances for the number of W. rintouli per quadrat were calculated for each treatment and the means were transformed to $\log_e$ to stabilize the variance. The null hypothesis, that the mean density of W. rintouli was not significantly different between the treatments, was tested using analysis of variance.

Sediments were sampled and analysed in the same way as described for the intertidal site, except that percent by weight of the primary mode (2ϕ) was also calculated. Student's t-test was used to compare the means of grain size indices, between the two controls.

Epifaunal Subtidal Experiment

Predator exclusion experiments for the epifaunal amphipod were conducted at Site 3 at Plantation Point (Figure 1). The amphipod H. rubra was abundant in the brown alga Caulocystis uvifera (C. Agardh) Areschough which occurred subtidally on siltstone. Caulocystis uvifera was a component of a mixed algal community of Sargassum spp. and Caulerpa cactoides (Turner) C. Agardh which was covered by about half a metre of water at low tide. The site was exposed to the prevailing summer north-easterly wind.

The experiment was a completely randomized design with three treatments (exclosure, control for exclosure effects and control for predation effects). There were six replicates of each treatment.

Predator exclusion bags 0.35 x 0.25 m were sewn from one mm fiberglass mesh, with a drawstring passing through a reinforced cloth base. Bags were placed over individual C. uvifera plants and the drawstring tightened to draw the bag around the base of the plant. The reinforced base of the bag was secured to the substratum by masonry nails hammered into the rock. Washers prevented the nail from

tearing through the fabric when wave action tugged at the bags. The corners of the bag were rounded to prevent amphipods becoming caught.

The control for exclosure effects due to physical changes in the environment, such as shading of the alga, and reduced current flow, consisted of bags with a large hole in each side and a drawstring which was tightened around the alga. The controls for predation effects were C. uvifera plants which were untouched until they were sampled at the end of the experiment.

A grid was drawn over a map of the study site and exclusion bags and controls randomly assigned positions on the grid.

The experiment was set up on 26th November 1983 and sampled after three weeks. Sampling was carried out by placing a 500 μm mesh sampling bag over each of the exclusion bags or control and pulling the C. uvifera plant from the substratum. The sampling bags were sealed and placed in 70% ethanol.

On return to the laboratory the contents of each sampling bag were washed in a 500 μm sieve. All crustaceans were washed or picked off the sampling bag and treatment mesh. The C. uvifera was placed in an elutriator (Berents, thesis paper b) and the remaining crustacea floated off the algae. Hyale rubra was sorted from the sample and counted under a binocular microscope. After carefully checking the algae to ensure the removal of all crustaceans, the volume of the algae was determined by displacement in water.

To allow for variable algal sample sizes, the data were analyzed as counts per unit volume of algae.

The null hypothesis that the mean numbers of H. rubra per unit volume of C. uvifera did not differ significantly between treatments was tested by analysis of variance for a completely randomized design using Genstat (Alvey et al., 1982). The number per unit volume was transformed to $\log_e$ (count +1) per unit volume to stabilize the variance. Fisher's protected least significant difference was used to compare treatment means following rejection of the null hypothesis.

Predators

At each site various methods were used to catch potential predators of U. metunqi, W. rintouli and H. rubra for gut contents analyses.

At the sandflat (Site 1), seine nets and hand spears were used to collect fish at high tide. Handspears, baited lines and fish traps were used to collect fish at the eight metre sandy bottom study site (Site 2). Other potential predators such as asteroids were also collected. Fish trawled by "FRV Kapala" in the vicinity of the study site were examined. At the subtidal algal site (Site 3), fish were collected using rotenone and baited lines.

RESULTS

Infaunal Intertidal Exclosures

The most abundant infaunal animal on the sandflat was U. metunqi. Another urohaustoriid amphipod Bumeralius buchalis Barnard & Drummond, soldier crabs Mictyris

longicarpus Latreille, gastropods Polinices sordidus (Swainson), bivalves Sanguinolaria donacioides (Reeve) and polychaetes Australonereis ehlersi (Augener) were found in low numbers.

The mean number of U. metungi per core and the mean density for each treatment were calculated at the completion of the experiment (Table I). Analysis of variance showed that there was no significant difference in the mean number of U. metungi per core between exclosures and controls ($F_{2,6} = 0.407$, $P > 0.05$).

There was no apparent change in the sediment in and around the exclosures or controls. On removal of the apparatus it was not apparent where the exclosures and controls had been placed. It had been feared that the scour plates surrounding the exclosures and controls could result in deoxygenation of the sediment beneath the plate but preliminary trials showed that the depth of the redox layer beneath the scour plates was the same as the surrounding sediment. Mean grain size in Phi (ϕ) units, skewness, sorting and percent silt-clay varied little between the cages and controls (Table II). Statistical

tests were not considered necessary. The sediment was course-medium sand with a negligible silt-clay content. It was well sorted and the distribution of sediment particle sizes was almost symmetrical.

The common stingray Urolophus testaceus (Muller & Henle) was the only species of fish caught which had U. metunqi in the gut contents. At the beginning of the experiment large numbers of U. testaceus were on the sandflat at high tide, and stingray feeding pits were frequently observed on the sandflat at other times of the year. The stingrays also fed on small penaeid prawns, polychaetes, and the bivalve S. donacioides. The gut contents of sand whiting Sillaqo ciliata Cuvier & Valenciennes and toad fish Torquigener hamiltoni (Gray & Richardson) were also examined but these fish ate bivalves, polychaetes, crabs and small penaeids.

Infaunal Subtidal Exclosures

Warraqaia rintouli was one of a diverse infaunal community dominated by peracarids and ostracodes.

At the end of the experiment there was a higher density of W. rintouli in the undisturbed sand (control for predation effects) than in the exclosures or exclosure controls (Table III). Analysis of variance showed that there was a significant treatment effect ($F_{2,6} = 17.894$, $0.001 < P < 0.005$). A comparison of the treatment means showed that the control for predation effects had significantly more W. rintouli than the exclosure or the control for exclosure effects.

The exclosures and controls for exclosure effects caused mounds of sediment to form inside the structures. Mean grain size, skewness, and percent silt-clay were not significantly altered by the experiment. The sediment in all treatments was course-medium sand with negligible silt-clay and an almost symmetrical distribution of particle sizes. Sorting and the percent by weight of the primary mode (2ϕ) were significantly different when comparing the sediments from the control for exclosure effects with those from the control for predation effects. The sediment from both types of controls was classified as moderately well sorted (Table IV).

The mullid Upenichthys lineatus (Bloch & Schneider) was the only species of fish caught which had W. rintouli in the gut contents. Other species of fish were caught which ate amphipods occurring with W. rintouli, but none contained remains identifiable as W. rintouli (Table V). The gut contents of two species of burrowing asteroids (Luidia australiae Doderlein and Echinocardium cordatum Muller & Troschel) were examined but these did not contain amphipods.

Epifaunal Exclosures

There was a significant difference between the transformed mean counts per unit volume of H. rubra between treatments (Table VI) ($F_{2,15} = 4.862$, $0.01 < P < 0.05$). A comparison of the treatment means showed that the density of H. rubra in the exclusion bags was significantly greater than the control for predation effects. The densities of H. rubra in the controls for predation effects and exclosure effects were not significantly different.

Gut contents analyses of fishes caught at Plantation

Point identified mado Atypichthys strigatus (Gunther) and weedfish Heteroclinus adelaidae (Castelnau) as predators of H. rubra. Other fish ate amphipods but the remains were unidentifiable (Table VII).

DISCUSSION

Infaunal Intertidal Exclosures

The design of the exclosures and controls resulted in no detectable modification of the microhabitat as indicated by sediment analysis and gross inspection.

Arntz (1977) had problems with drifting algae which caught on the outside of cages and caused deoxygenation. In the experiment in Currambene Creek some drifting Ecklonia radiata (C.Agardh) J. Agardh and seagrasses fouled on the cages and the anchoring guy ropes but were removed during daily inspections of the study site. The exclosures and controls did not require scrubbing to remove fouling growth from the mesh because of the short duration of the experiment and daily exposure at low tide. Doherty & Sale (1985), Gee et al. (1985) and Leber (1985),

also adopted a caging period of one month or less, to reduce the effects of fouling and algal growth.

Virnstein (1978), Hulberg & Oliver (1980) and Doherty & Sale (1985) described a "reef effect" in some caging experiments, which is the tendency for cages to attract fishes. At high tide the experiment at Currambene Creek was covered by up to one metre of water but an increase in the numbers of fish around the cages was not observed.

Shorebirds were not observed on the sandflat and are unlikely to prey on U. metunqi although many species of waders were seen feeding on the mudflats and seagrasses downstream from the study site. Quammen (1982) also found that shallow-feeding shorebirds were not important predators on the infauna of sandy habitats.

Infaunal animals such as polychaetes have been shown to prey on other infaunal species (Commito, 1982; Ambrose, 1984a & b; Ronn et al., 1988). The cage design of this experiment did not exclude infaunal predators, however, at the Currambene Creek sandflat there were no potential infaunal predators

Predation studies in the northern hemisphere have identified crabs as predators of infaunal species (Virnstein, 1977; Reise, 1978; Quammen, 1984). The only species of crab resident on the sandflat was Mictyris sp. (pers. obs.) which feeds on organic debris and diatoms (Cameron, 1966). Portunus pelagicus Linnaeus, the blue swimmer crab which was common in Currambene Creek, may be a predator of U. metungi because it feeds on invertebrates including amphipods (Williams, 1982). These crabs, however, would have been excluded by the cages.

The results showed no significant difference in the density of U. metungi between treatments, and I conclude that although Urolophus testaceus was identified as a predator of the amphipod U. metungi, it had no significant effect on amphipod abundance. The exclosures effectively excluded all suspected predators and did not introduce artifacts. I conclude that predation is not an important structuring factor on the abundance of U. metungi.

Infaunal Subtidal Experiment

The results of this experiment were confounded by artifacts of the experiment itself.

The substratum was visibly altered although sediment analyses revealed only minor changes. Although the index for sorting was significantly different between the control for exclosure effects and the undisturbed sediment, both were classed as moderately well sorted (Gray, 1981). The percent by weight of the primary mode (2ϕ) was also significantly different between the control for exclosure effects and the undisturbed sediment. Nothing is known of W. rintouli's tolerance to changes in sediment grain sizes and statistically significant differences may or may not be biologically significant.

The mesh of the exclosures and control accumulated algal growth and a deposit of fine organic matter which settled out of the water. The mesh was cleaned by scrubbing, but this disturbed the surrounding environment and attracted fish.

Another artifact of the experiment was the "reef effect" described by Virnstein (1978), Hulberg & Oliver (1980) and Doherty & Sale (1985). Fishes seemed more abundant in the vicinity of the exclosures and controls, especially at night. The control for exclosure effects allowed predators to feed on the sediment but may have attracted more predators than undisturbed sand. During the experiment a numb ray Hypnos monopterygium (Shaw & Nodder) was observed buried in the sand inside a control.

Another factor in explaining the low mean density in the exclosures and exclosure controls may have been infaunal predation (eg. Commito, 1982; Ambrose, 1984a & b; Ronn et al., 1988). The exclosures did not protect W. rintouli from infaunal predators such as polychaetes.

The scour plates at this site were not as effective at preventing scour as at the intertidal site. On occasions scour occurred at the edge of the cage and goatfish Upenichthys lineatus and yellowtail Trachurus novaezelandiae Richardson swam under the scour plate into the cage. The cages were inspected daily and on those occasions when fish entered the cage, the cage was lifted

and the fish removed. Upenichthys lineatus was shown to be a predator of W. rintouli and may have fed on the infauna while trapped.

The very low numbers of W. rintouli in the exclosures and controls may have been caused by any of these factors. It is not possible to draw any conclusion about the effects of predation on the abundance of W. rintouli, although goatfish U. lineatus which were predators of W. rintouli, were abundant at the study site and appeared to feed on the bottom almost continuously. Juvenile yellowtail T. novaezelandiae and juvenile snapper Chrysophrys auratus (Bloch & Schneider) were often observed feeding on infauna but the specimens collected did not contain identifiable W. rintouli.

The use of scour plates was successful at the intertidal site but not at the eight metre depth site. This may have been because of increased water movement or the fouled mesh may have offered a more effective barrier to water movement and increased the scour effect. Wider scour plates may be more effective in this environment.

Epifaunal Exclosures

The uneven rocky bottom and exposed position of Plantation Point meant that cages were unsuitable as predator exclosures. Mesh bags were used to exclude predators from the epifauna of C. uvifera. This is a new technique for predator exclusion. The bags appeared to fit into the habitat with little modification of the environment. They swayed in the swell in the same way as the algae, they did not appear to attract predators, nor did the alga which was contained inside appear to deteriorate.

Caulocystis uvifera harboured a diverse epifaunal community which was dominated by gammaridean and caprellidean amphipods. Hyale rubra is one prey species among many, and gut contents analyses revealed that other amphipods such as Eusiridae (Tethygeneia sp.), Ampithoidae, Melitidae (Ceradocus sp.) and Dexaminidae are prey for predatory fishes (Table VII). Two species of fishes were identified as predators of H. rubra and others contained unidentifiable amphipod parts. Bell (1979) identified the red morwong Cheilodactylus fuscus Castelnau

on rocky reefs in Sydney as a predator of Hyale sp.

The results showed that C. uvifera protected by exclusion bags had significantly more H. rubra than did C. uvifera exposed to predation. This suggested that predation on amphipods in C. uvifera decreased amphipod densities. The mean densities of H. rubra in the two types of controls were not significantly different which suggested that the bag with large holes to allow access by predators provided the same habitat as unenclosed algae. However, the mean density of H. rubra in the exclusion bags was not significantly different from that in control for exclusion effects. The variance for the exclusion bags was high, and more replicates may have been necessary to reduce Type II error and give a significant difference from the control for exclosure effects (Toft & Shea, 1983).

I conclude that predation did affect the abundance of H. rubra and that exclusion bags are a technique of predator exclusion that deserves further investigation.

The results of these field experiments show that predation reduced epifaunal amphipod abundance but not infaunal amphipod abundance. Hence evidence is provided for differential risk of predation for amphipods living in sandy and algal habitats. This result is similar to that of Young & Young (1977) and Nelson (1979 a & b) who examined the effect of predation on amphipods in seagrass communities. They concluded that the effect of predation within the community was greater for epifaunal than infaunal amphipods.

Van Dolah & Bird (1980) postulated that differential adult mortality risk from predation influenced reproductive patterns in infaunal and epifaunal amphipods but evidence was lacking to test this hypothesis. These field experiments provide evidence for differential predation risk, and further work will examine the reproductive patterns of U. metungi, W. rintouli and H. rubra.

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Table I. Mean number of Urohaustorius metunqi per core taken in exclosures and controls at Site 1 in Currambene Creek after three weeks. Underline indicates no significant difference between treatment means.

	Control (predation effects)	Exclosure	Control (exclosure effects)
Mean Value	20.61	24.2	26.3
Standard Error	2.07	2.68	3.23

Table II. Sediment analysis for exclosures and controls at Site 1 at Currambene Creek (n = 2; $\phi = -\log_2$).

Treatment	Mean of mean grain size ± SE ϕ units	Mean sorting ± SE ϕ units	skewess ± SE ϕ units	% silt/ clay
Exclosure	1.6 ± 0	0.46 ± 0.02	0.04 ± 0.04	0.02 ±0.01
Control (Exclosure Effects)	1.6 ± 0.1	0.45 ± 0.01	0.01 ± 0.01	0.1 ± 0
Control (Predation Effects)	1.7 ± 0	0.46 ± 0.02	0.04 ± 0.04	0.01 ±0.01

Table III. Mean numbers of Warragaia rintouli per quadrat sampled at Site 2 in exclosures and controls after three weeks. Underline indicates no significant difference between treatment means.

	Control (predation effects)	Exclosure	Control (exclosure effects)
Mean value	11.25	1.33	0.33
Standard error	2.06	0.26	0.14

Table IV. Sediment analysis for exclosures and controls at Site 2. Student's t-test was performed on the means for controls to test the null hypothesis that there was no significant difference between the grain size indices ($\phi = -\log_2$).

Treatment	Mean of mean grain size ϕ units	Mean sorting ϕ units	Mean skewness ϕ units	Mean % by weight of primary mode (2ϕ)	Mean % silt/clay
Exclosure n = 1	1.8	0.62	-0.1	47.2	0.1
Control (Exclosure Effects)	2.0	0.52	0.1	43.3	0.1
1 SE n=2	0.1	0	0.1	0.4	0
Control (Predation Effects)	1.8	0.67	-0.1	50.4	0.1
1 SE n=2	0	0	0	0.3	0
	NS	0.01<P<0.05	NS	P<0.01	

Table V. List of fishes caught at Site 2 off Moona Moona Creek. (number of fish examined : size range in cms)

Fish with Warragaia rintouli in guts:

Upenichthys lineatus (Bloch & Schneider) (goatfish)	(1 : 10.2)

Fish with other amphipods in guts:

Acanthopagrus australis (Gunther) (yellowfin bream)	(2 : 12.2-12.3)
Platycephalus longispinis Macleay (longspined flathead)	(3 : 11.2-18.5)
Upenichthys lineatus (Bloch & Schneider) (goatfish)	(1 : 10.0)
Pardachirus hedleyi Ogilby (peacock sole)	(1 : 9.5)
Chrysophrys auratus (Bloch & Schneider) (snapper)	(1 : 9.8)
Atypichthys strigatus (Gunther) (mado)	(3 : 9.8-10.8)

Fish with no amphipods in guts:

Trachurus novaezelandiae (Richardson) (yellowtail)	(1 : 11.5)
Acanthopagrus australis (Gunther) (yellowfin bream)	(2 : 8.7-12.4)

Table VI. Comparison of mean number of Hyale rubra per unit volume of Caulocystis uvifera between exclusion bags and controls at Site 3 at Plantation Point. Underline indicates no significant difference between treatments.

	Control (predation effects)	Control (exclusion effects)	Exclusion bags
Mean Value	0.29	0.80	3.36
Standard Error	0.12	0.35	1.32

Table VII. List of fishes caught in subtidal algae at Site 3 at Plantation Point. (number of fish examined : size range in cms)

Fish with *Hyale rubra* in guts:	
Heteroclinus adelaidae (Castelnau) (weedfish)	(1 : 3.2)
Atypichthys strigatus (Gunther) (mado)	(2 : 2.2-3.0)
Fish with other amphipods in guts:	
Acanthopagrus australis (Gunther) (yellowfin bream)	(1 : 18.0)
Pelates quadrilineatus (Bloch) (therapon)	(3 : 8.5-9.5)
Suezichthys sp. (wrasse)	(1 : 7.3)
Heteroclinus adelaidae (Castelnau) (weedfish)	(1 : 3.8)
Centropogon australis (White) (fortesque)	(1 : 2.5)
Fish with no amphipods in guts:	
Sphyraena novaehollandiae Gunther (snook)	(1 : 16.5)
Pelates quadrilineatus (Bloch) (therapon)	(1 : 9.0)

LEGENDS FOR FIGURES

Figure 1. Map of Jervis Bay showing location of study sites:
1. Infaunal intertidal study site in Currambene Creek
2. Infaunal subtidal study site in 8m depth
3. Epifaunal subtidal study site at Plantation Point

Figure 2. Exclosures and scour plates used for infaunal experiments.

Figure 1. Map of Jervis Bay showing location of study sites:

1. Infaunal intertidal study site in Currambene Creek
2. Infaunal subtidal study site in 8m depth
3. Epifaunal subtidal study site at Plantation Point

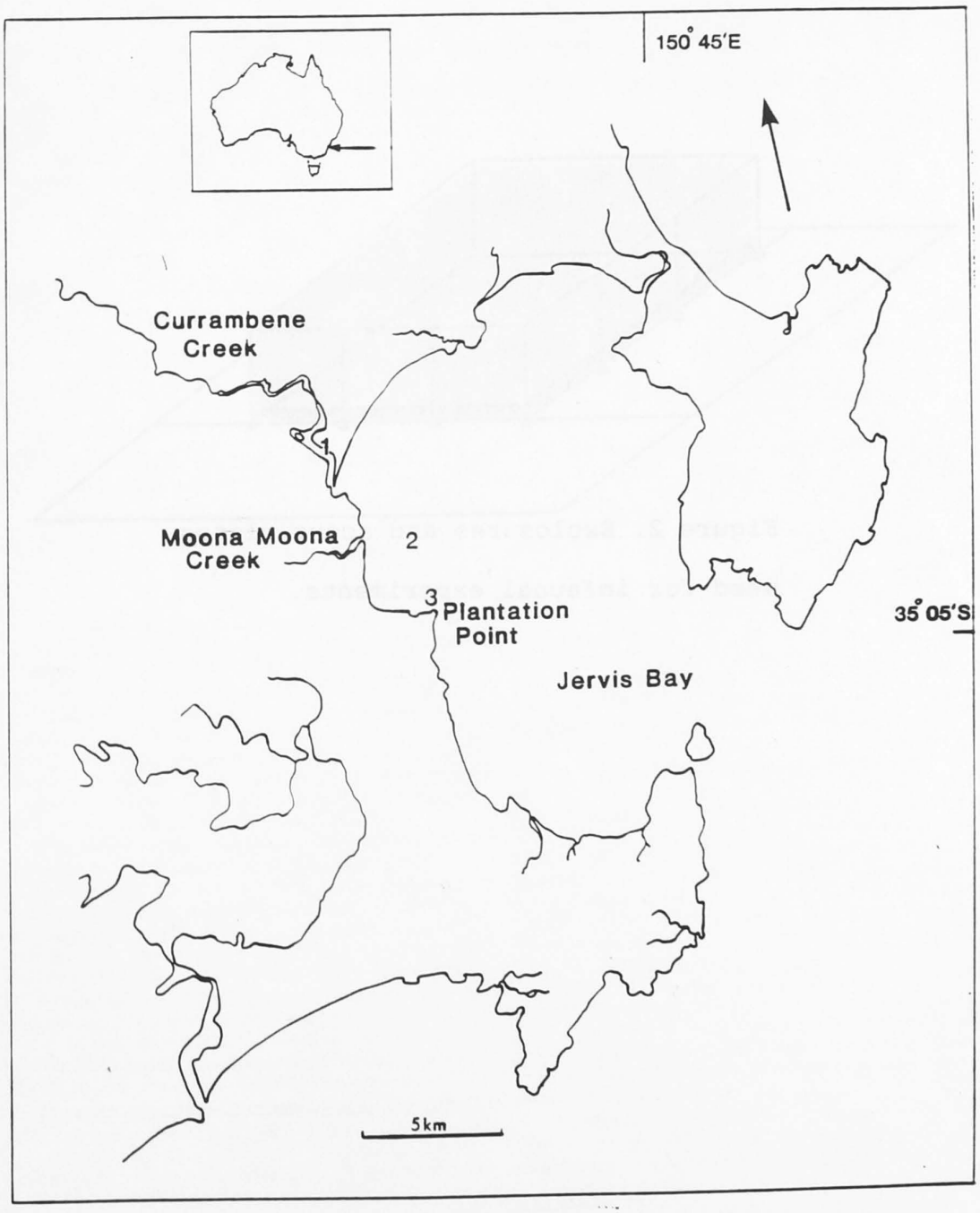
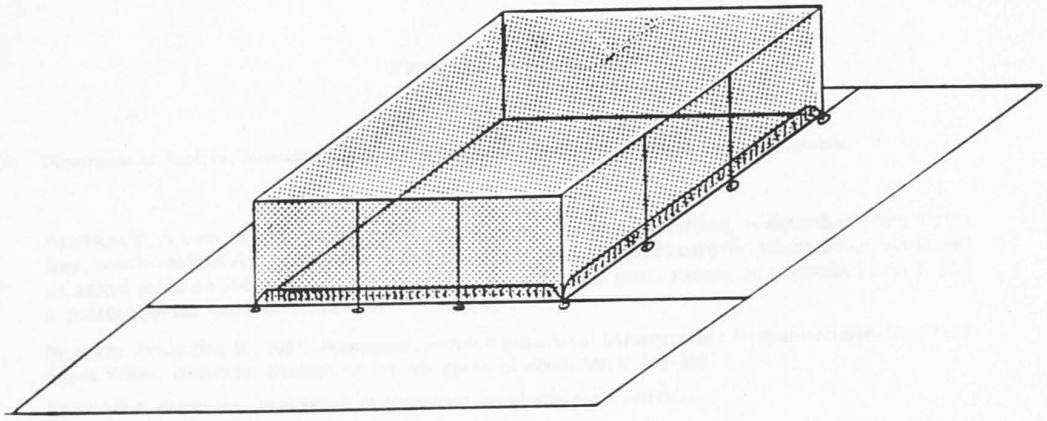

150° 45'E
Currambene Creek
Moona Moona Creek
1
2
3
Plantation Point
35° 05'S
Jervis Bay
5km

Figure 2. Exclosures and scour plates used for infaunal experiments.



Records of the Australian Museum (1985) Vol. 36: 253-258. ISSN-0067-1975

Warragaia rintouli n.gen., n.sp. (Amphipoda: Urohaustoriidae) from New South Wales, Australia.

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ABSTRACT. A new urohaustoriid genus and species, *Warragaia rintouli*, is described from Jervis Bay, south-eastern Australia. *Warragaia rintouli* is the only urohaustoriid which never has spines or apical setae on the dactyl of peraeopod 5, has a vestigal inner ramus on uropods 1 and 2, and a posterodorsal hook on coxa 7.

BERENTS, PENELOPE B., 1985. *Warragaia rintouli* n.gen., n.sp. (Amphipoda : Urohaustoriidae) from New South Wales, Australia. Records of the Australian Museum 36(5): 253-258.

KEYWORDS: taxonomy, urohaustoriid amphipod, south-eastern Australia.

Urohaustoriids are fossorial amphipods in the superfamily Haustorioidea. Barnard & Drummond (1982) revised the Haustorioidea and erected the family Urohaustoriidae based on collections from Australia.

While studying the life histories of a number of species of amphipods in Jervis Bay, New South Wales, I found a urohaustoriid which could not be assigned to genus. This species has some characters in common with each of three genera described by Barnard & Drummond (1982): *Tottungus*, *Tuldarus* and *Dirimus*.

The diagnosis of *Warragaia* follows the form established by Barnard & Drummond (1982) for urohaustoriids. The length of the whole animal was measured along the mid-dorsal line from the tip of the rostrum to the base of the telson. The method described by Barnard & Drummond (1978) was used for measuring dissected parts. Barnard & Drummond (1982) defined a formula for describing patterns of spines and setae. A modified formula is used herein : E = long or short seta, S = long or short spine.

Material is lodged in the Australian Museum, Sydney, (AM) and the Museum of Victoria, Melbourne, (NMV).

The following abbreviations are used in the figures: A1, 2: antenna 1, 2; G1, 2: gnathopod 1, 2; C3, 4: coxa 3, 4; MD: mandible; MX1, 2: maxilla 1, 2; MP: maxillipeds; P3-7: peraeopod 3-7; T: telson; U1-3: uropod 1-3; l: left; r: right.

Warragaia n.gen.

Diagnosis. Rostrum weak, but head large and cowl-like. Primary flagellum of antenna 1 elongate, accessory flagellum weak. Outer plate of maxilla 1 with 9 spine teeth. Mandibular incisors truncate; right and left laciniae mobiles dissimilar; 1 spine blade on right mandible, 2 spine blades on left mandible. Maxillae 1 and 2, and maxillipeds lacking baler lobes. Coxae 1 and 2 small, coxa 1 larger than coxa 2. Coxae 3 and 4 large, coxa 3 subequal to coxa 4, posteroventral setae small. Coxa 4 without setae. Gnathopod 2 subchelate. Dactyls of peraeopods 5-7 lacking spines, and subapical and apical setae in both males and females. Article 2 of peraeopod 5 strongly expanded; article 2 of peraeopods 6 and 7 of moderate width. Pleopod 3 smaller than pleopod 2. Epimeron 1 scarcely differentiated; epimera 2 and 3 of similar size, lacking setae. Peduncle of uropods 1 and 2 sparsely setose laterally. Uropod 1 outer ramus with 2-3 plumose apical setae; inner ramus very reduced, fused to peduncle. Uropod 2 outer ramus with 1-2 plumose apical setae; inner ramus very reduced, fused to peduncle. Uropod 3 outer ramus larger than inner ramus, 2-articulate, with 1-2 plumose apical setae. Telson short, entire, wider than long.

Type-species. *Warragaia rintouli* n.sp.

Etymology. *Warragaia* is derived from an aboriginal word, 'warragai', meaning 'plenty of sand'. The gender is feminine.

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Warragaia rintouli **n.sp.**

Figs 1–3

Type-material. HOLOTYPE, male, 1.76 mm, AM P34773; ALLOTYPE, 1.64 mm, AM P34774; 48 PARATYPES, AM P34775; 1 PARATYPE, NMV J10779; 1 km off Moona Moona Creek, Jervis Bay, New South Wales, Australia, 35°03'S, 150°41'E, airlifted sand and shelly sand, 8 m, P.B. & P.M. Berents, 17 November, 1981.

Additional material. Sixty-two specimens, AM P34776, as for holotype, 18 February, 1983; 9 specimens NMV J10780, as for holotype, 29 April, 1983.

Description. Holotype male, 1.76 mm. *Head* about 0.8 times as long as wide. *Antenna 1*: peduncle 1.3 times as long as flagellum; flagellum 9-articulate, each article bearing aesthetascs; accessory flagellum 3-articulate. *Antenna 2*: articles 4 and 5 of peduncle with mid-dorsal armature dominated by spines, article 4 SESSESSSSSSESS, article 5 SSSSESS; flagellum 6-articulate.

Mandible: incisor truncate; right lacinia mobilis narrow, spatulate (may be obscured by curved edges of incisor); left lacinia mobilis triangular with two apical teeth; 1 spine blade on right mandible, 2 spine blades on left mandible; molar triturating; palp 3-articulate, article 1, 0.4 times as long as article 2, articles 2 and 3 subequal, article 3 with 3 awned spines and 3 shorter simple spines. *Maxilla 1*: inner plate linguiform with 1 sub-apical plumose seta; outer plate truncate bearing 9 spine teeth; palp with 3 apical plumose setae. *Maxilla 2*: inner plate ovate with apical setae and submarginal setae; outer plate truncate, with apical setae. *Maxillipeds*: inner plate with medial plumose seta, bearing apical plumose setae and stout spines; outer plate with setal/spine formula E-EESEEESESS-E; palp 4-articulate, inner margin of article 2 densely setose, dactylus slender with 3 setae and apical spine.

Gnathopod 1: simple; coxa extended anteroventrally; article 2 slender; article 5 expanded, posterior margin setose; article 6, 0.6 times as long as article 5, distally setose; dactylus slender with setule. *Gnathopod 2*: subchelate; coxa smaller than coxa 1; article 2 slender, posterior margin with long setae; article 3 bearing long setae with terminal pectination; article 5 elongate, posterior margin sparsely setose; article 6, 0.7 times as long as article 5, palm setose, confluent with posterior margin; dactylus recurved with setule on inner margin.

Peraeopod 3: coxa large, 1.2 times as wide as long, anteroventral corner broadly rounded, posteroventral corner drawn to subacute point; article 5 posterior margin with 3 stout spines, distal margin bearing sharp denticles; article 6 subequal to article 5, with 7 stout spines, distal margin bearing sharp denticles; dactylus slender, 1.4 times as long as article 6, cusp near apex. *Peraeopod 4*: similar size and proportions to peraeopod 3 except coxa quadrate. *Peraeopod 5*: coxa 1.5 times as wide as long; article 2 broadly expanded, almost as wide as long; articles 3–6 with groups of spines; article 5 subequal in length to article 6; dactylus slender, armed with denticles, 0.8 times as long as article 6, plumose setule at M 30, cusp near apex. *Peraeopod 6*: longer and less spinous than peraeopod 5; coxa 1.4 times as wide as long; article 2 moderately expanded, 0.6 times as wide as long, anterior margin bearing 4 groups of spines; article 4 posterior margin with 2 long plumose setae; articles 4–6 with groups of spines; dactylus slender, setule at M 41, cusp near apex. *Peraeopod 7*: similar size and proportions to peraeopod 6 except coxa with posterodorsal hook; article 2 anterior margin with 3 spines; article 4 without long plumose setae.

Pleopods: peduncles of all pleopods short, wider than long; inner rami shorter than outer rami; pleopod 3 shorter than pleopod 2.

Epimeron 1: scarcely differentiated. *Epimera 2 and 3*: similar in size, lacking setae, postero-ventral margins rounded.

Uropod 1: peduncle with 3 plumose setae laterally; inner ramus very reduced, fused to peduncle, bearing 1 plumose apical seta; outer ramus with 2 plumose apical setae, 2 plumose setae along inner margin. *Uropod 2*: similar to uropod 1 except peduncle without lateral setae. *Uropod 3*: inner ramus with 2 apical plumose setae, inner margin with 3 plumose setae; outer ramus 2-articulate, 1 apical seta. *Telson*: entire, wider than long.

Allotype female, 1.64 mm. Similar to holotype except in following ways: *Antenna 1*: article 1 of peduncle with 3 stout mid-dorsal brush setae; primary flagellum 6-articulate, aesthetasc on articles 5 and 6. *Antenna 2*: formula for facial armature of article 4 SSESSSSSSESS, article 5 SSESS. *Maxillipeds*: outer plate with setal/spine formula E-EESEEESESESE. *Peraeopod 7*: article 2 anterior margin with 4 spines. *Uropod 1*: peduncle with 2 plumose setae laterally. *Uropod 3*: inner margin of inner ramus with 2 apical setae; outer ramus bearing 2 apical setae.

Largest male: 1.92 mm. Largest female: 2.32 mm (ovigerous).

Variation. *Antenna 1*: most specimens have 3 stout mid-dorsal brush setae on article 1 of peduncle as described for allotype. *Antenna 2*: the facial armature of article 4 of peduncle varies although spines are dominant. The formulae are characterized by a middle group of 6 or 7 spines followed by ESS (occasionally ESSS). The proximal end varies from ESESSE to SSE. *Maxillipeds*: outer plate may have 4 or 5 spines. *Gnathopod 2*: palm may be more setose in large females. *Peraeopod 3*: article 6 may have 6 or 7 stout spines. *Peraeopods 6 and 7*: dactylus occasionally with setule at cusp. *Uropod 1*: outer ramus bearing 2 or 3 plumose apical setae. *Uropod 2*: outer ramus bearing 1 or 2 plumose apical setae. *Uropod 3*: outer and inner rami with 1 or 2 plumose apical setae. The number of groups of lateral setae on the inner and outer margins is variable.

Etymology. The species is named for Ian Rintoul, 13/12/50–26/3/84.

Remarks. *Warragaia rintouli* belongs to the group of urohaustoriid genera without spines on the dactyl of peraeopod 5 and with a weak accessory flagellum. The other genera in this group are *Dirimus*, *Tottungus* and

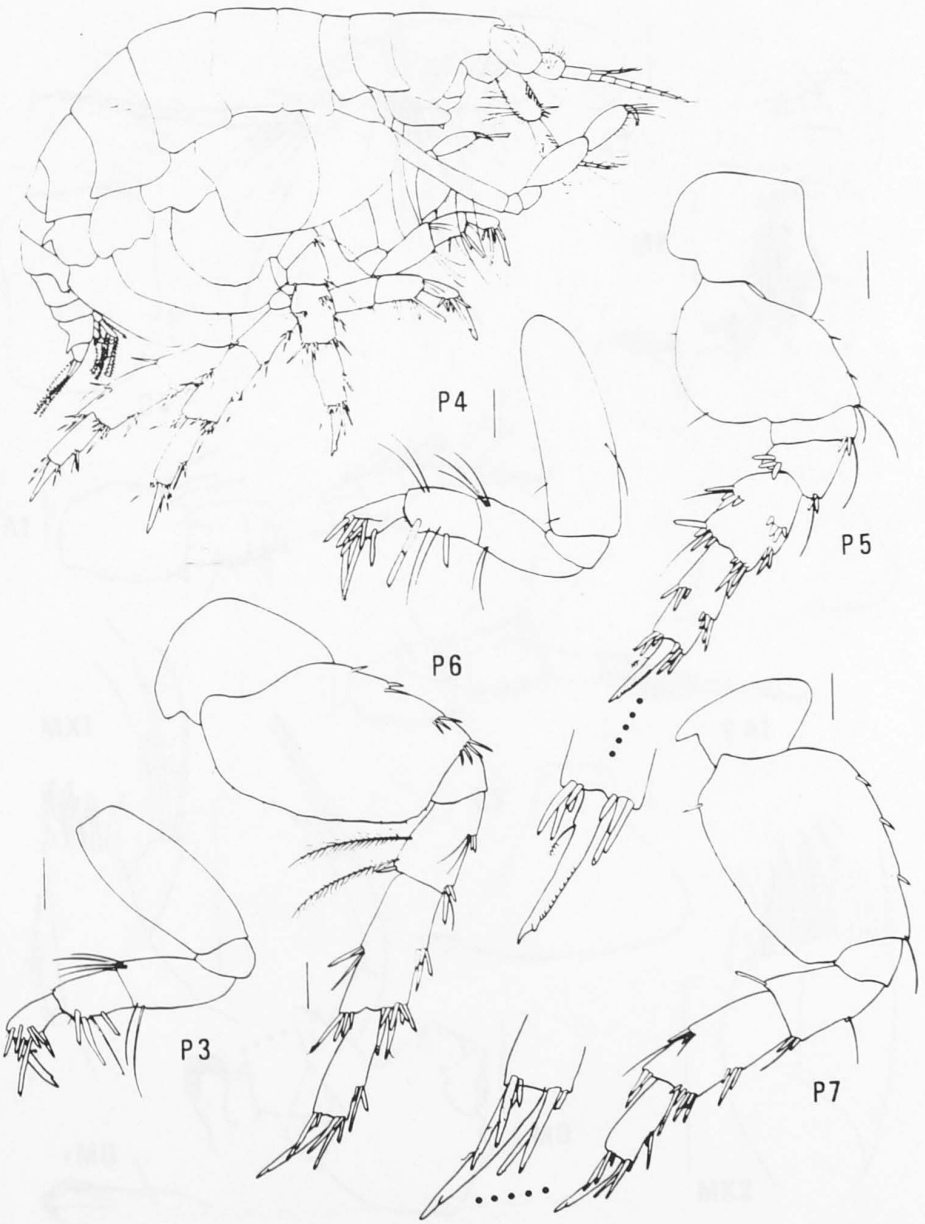

Fig. 1. *Warragaia rintouli* n.gen. n.sp.: whole animal, paratype, female, 1.92 mm; peraeopods, holotype, male, 1.76 mm. Jervis Bay, N.S.W., Australia. **Scale** represents 0.1 mm.

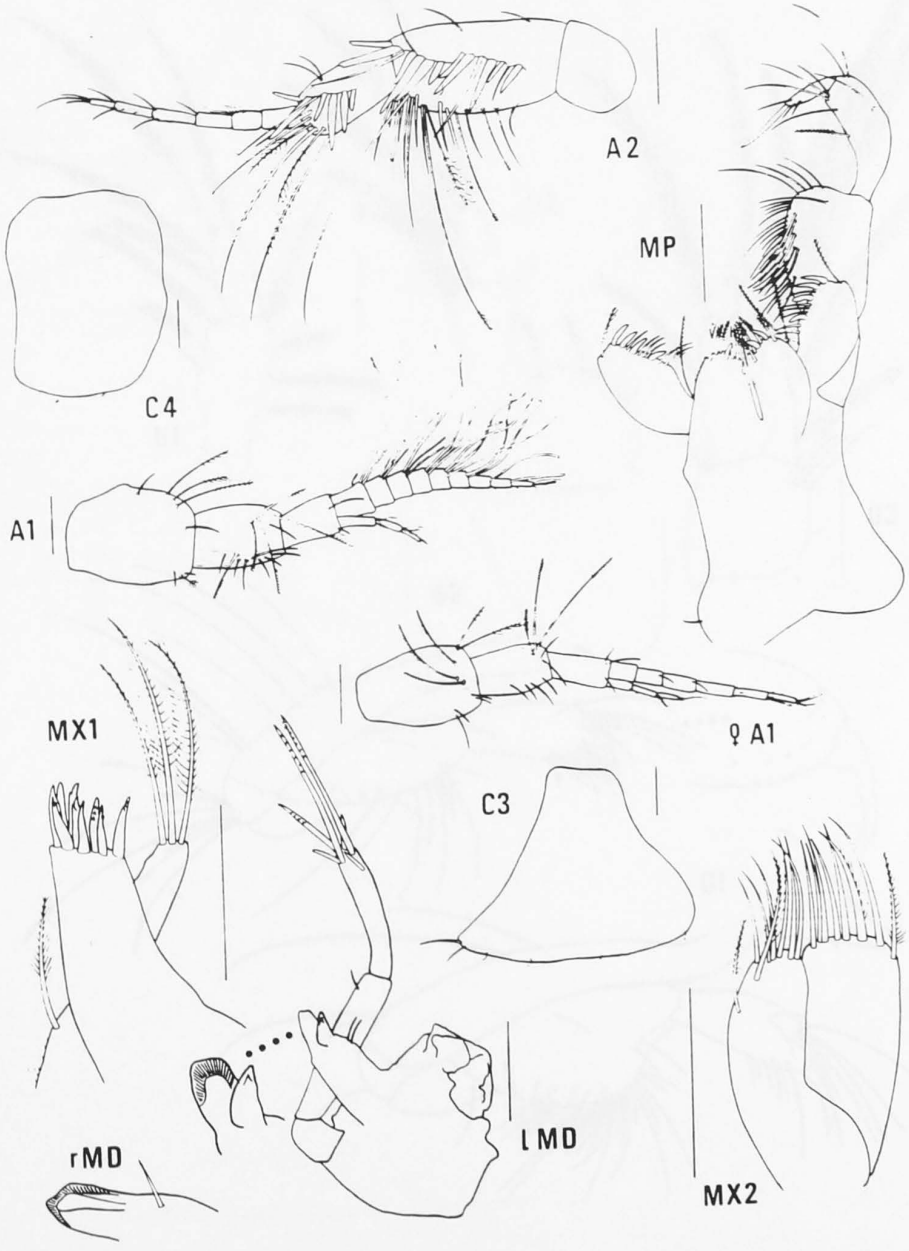

Fig. 2. *Warragaia rintouli* n.gen. n.sp.: holotype, male, 1.76 mm; allotype, 1.64 mm. Jervis Bay, N.S.W., Australia. Scale represents 0.1 mm.

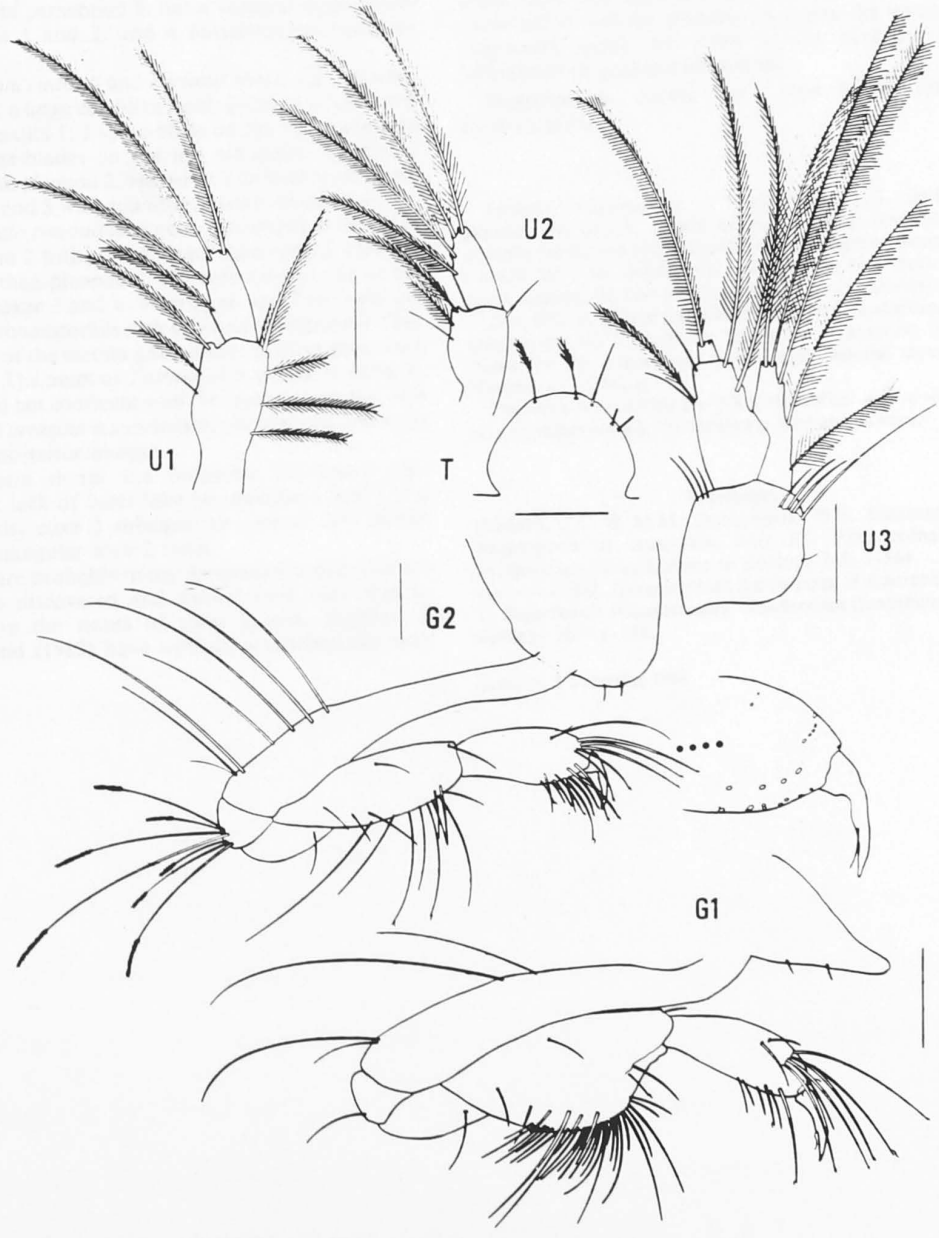

Fig. 3. *Warragaia rintouli* n.gen. n.sp.: holotype, male, 1.76 mm. Jervis Bay, N.S.W., Australia. **Scale** represents 0.1 mm.

Tuldarus. *Warragaia rintouli* shares other diagnostic characters with each of the above genera and has some unique characters. *Warragaia rintouli* is the only urohaustoriid which never has spines or apical setae on the dactyl of peraeopod 5, has a vestigial inner ramus on uropods 1 and 2, and a posterodorsal hook on coxa 7.

Warragaia rintouli and *Dirimus* share the following characters: a large cowl-like head; 9 spines on the outer plate of maxilla 1; 1 spine-blade on the right mandible and 2 spine-blades on the left mandible; pleopod 3 smaller than pleopod 2; epimeron 2 lacking facial setae; epimera 2 and 3 with rounded posteroventral margins.

Warragaia rintouli resembles *Tottungus* in the small coxae 1 and 2 with coxa 1 larger than coxa 2; pleopod 3 smaller than pleopod 2; the reduction in size of the setae on coxae 3 and 4. *Warragaia* and *Tottungus* are the only urohaustoriids with subchelate gnathopod 2 but the palms of the second gnathopods in these genera are different. The palm of *Tottungus* is almost transverse, serrate and not confluent with the posterior margin. The palm of *Warragaia* is subchelate, smooth and confluent with the posterior margin.

Warragaia shares the following characters with *Tuldarus*: lack of baler lobe on maxillae 1 and 2 and maxillipeds; coxa 3 subequal to coxa 4; left lacinia mobilis triangular with 2 teeth.

There are probably many Australian urohaustoriids yet to be discovered and future work may lead to changes in the status of these genera. Barnard & Drummond (1982) have worked predominantly with collections from Westernport and Port Phillip Bay (Victoria), plus some material from Moreton Bay (Queensland) and the Hunter River district (NSW). The urohaustoriids from the remainder of the Australian coast have not been studied. As more material is examined it will be possible to assess the value of characters which are used in the diagnoses of urohaustoriid genera and species.

Distribution. Jervis Bay, New South Wales (type-locality).

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AMPHIPOD LIFE HISTORY STRATEGIES AND THE CONSTRAINTS OF BODY SIZE

Van Dolah and Bird's (1980) hypothesis stated that "adult mortality risk is correlated positively with egg number and inversely with egg size". The hypothesis predicted that epifaunal amphipods will have more and smaller eggs than infaunal amphipods of comparable size. They proposed that infaunal and epifaunal amphipods have similar reproductive output (represented by brood volume) but epifaunal species divide their reproductive output as many small eggs whereas infaunal amphipods have a few large eggs because of the risk of predation associated with epifaunal life. Van Dolah and Bird argued that it is advantageous for epifaunal amphipods to have smaller eggs because development time is correlated with egg size. A short development time reduces the length of time eggs are held in the brood pouch, which in turn reduces the probability of offspring being eaten while in the brood pouch. For epifaunal amphipods adult mortality risk is an important component of reproductive fitness.

Van Dolah and Bird (1980) conceded that more rigorous tests of infaunal and epifaunal amphipod reproductive patterns were needed among species living at equivalent latitudes, combined with evidence of differential mortality risk.

Predation

I tested Van Dolah and Bird's hypothesis for infaunal and epifaunal amphipods at Jervis Bay. The relative risk of predation in the infaunal and epifaunal habitats was assessed using exclosures. The results of these experiments showed that predation reduced the density of Hyale rubra but did not affect the density of Urohaustorius metungi. Unfortunately the results were inconclusive for Warragaia rintouli because of artefacts of the experiment. Exclusion experiments in seagrass communities have also shown that predators had a greater effect on epifaunal amphipods than infaunal amphipods (Young and Young, 1977; Nelson, 1979a and b).

My experiments established that predation affected the density of the epifaunal amphipod H. rubra but not the

infaunal amphipod U. metunqi, although predators of both species were identified in their respective habitats. Differential mortality risk from predation has thus been established for H. rubra and U. metunqi. The underlying assumption of Van Dolah and Bird's hypothesis, that epifaunal amphipods are more at risk from predation than infaunal amphipods, has therefore been satisfied for these two species.

Van Dolah and Bird's hypothesis only considered infaunal and epifaunal amphipods. I have enlarged the scope of the model to test the hypothesis in another habitat. I considered that an endocommensal amphipod such as Leucothoe commensalis which lived in the ascidian Herdmania momus, would be less at risk from predation than epifaunal and infaunal amphipods, and therefore the predictions of Van Dolah and Bird's hypothesis could be tested in another habitat. The hypothesis predicts that L. commensalis would have fewer large eggs than an infaunal amphipod of comparable size.

The effect of predation on infaunal and epifaunal amphipods was compared using exclosures, however it was

not possible to use this technique for Leucothoe commensalis living in the ascidian Herdmania momus. There was no synchrony between the populations of L. commensalis in ascidians, and on all sampling occasions there were ascidians with few L. commensalis and others with many L. commensalis. Destructive sampling was the only way to determine the population of commensals within a host, therefore there was no way of establishing adequate controls for the experiment. If synchrony had been present in the population, the same experimental design as that used for Hyale rubra could have been used to exclude predators and control for treatment effects.

Predation is unlikely to be an important structuring factor for L. commensalis living within the ascidian. The tunic of Herdmania momus is tough and embedded with spicules. Young (1986) has shown that both of these features deter predators. Predation may be an important factor for free-living L. commensalis, but it is not known whether mature adults are found outside the host. Since Van Dolah and Bird's hypothesis makes predictions about adult mortality risk and reproductive output, predation on immature L. commensalis outside the host would not alter

the predictions made by the hypothesis.

Life Histories

The other aspect of the test of Van Dolah and Bird's hypothesis was to describe the reproductive patterns of U. metunqi, W. rintouli, H. rubra and L. commensalis, and compare egg size and number.

(i) Comparison of Results

(a) Egg Size

Egg size is an important trait in life history models because for many invertebrate groups it is a correlate of development pattern (Menge, 1975; Strathmann, 1977; Turner and Lawrence, 1979; Grahame and Branch, 1985). However, all gammarideans have direct development so this aspect of life history theory does not apply to the study of gammaridean reproductive patterns.

Amphipod egg sizes range from 0.30 mm to 1.75 mm (Nelson, 1980), so all of the study species have small eggs compared with other gammarideans (Table 1).

A comparison of mean egg size among the four study species showed that the eggs of the infaunal amphipod Urohaustorius metungi were significantly larger than the other three species, and L. commensalis eggs were significantly larger than W. rintouli and H. rubra. There was no significant difference in mean size between the eggs of W. rintouli and H. rubra (anova on $\log_e$ transformed mean egg sizes, $F_{3,76} = 99.957$).

Steele and Steele (1975a) found that egg size in Gammarus could be used to predict size at maturity, reproductive cycle, geographic distribution and fecundity. Larger mean egg sizes have also been shown to be correlated with larger mean brood size and larger mean size of reproductive females (Nelson, 1980). However, the data herein show that egg size is not always a good predictor of female size and brood size. There is no significant correlation between egg size and brood size ($r = .8294$, 2 df) and egg size and size of reproductive females ($r = .7878$, 2 df). Because egg size and brood size are dependent variables, comparisons of reproductive patterns among species should take both variables into

consideration. Van Dolah and Bird's hypothesis made predictions about both egg size and number.

(b) Egg Size and Number

There was no significant difference between the mean length of ovigerous females of U. metunqi (3.50 mm) and H. rubra (3.65 mm) ($t = 1.6692$, $df = 152$), so direct comparisons can be made of egg size and number. Such comparisons show that there was no significant difference in brood size, ie. number of eggs, ($t = 1.6095$, $df = 156$) between U. metunqi and H. rubra, however, U. metunqi had significantly larger eggs than H. rubra.

These results show that infaunal and epifaunal amphipods of similar length can have broods with the same egg number with different size eggs which produce hatchlings of the same length (Table 1). This result does not corroborate the hypothesis of Van Dolah and Bird (1980). Hyale rubra has smaller eggs than U. metunqi as predicted by the hypothesis, but does not have more eggs.

This result appears to contradict the accepted inverse

relationship between the dependent variables egg size and brood size in brooding crustacea of the same size (Steele and Steele, 1975a; Mauchline, 1988).

The apparent contradiction arises through the use of a linear measure, such as total length, as a measure of female size. Urohaustoriids are broad-bodied amphipods which have a larger brood pouch capacity than narrow-bodied hyalids of the same length. Total length is not necessarily the best indication of brood chamber capacity. In comparing the way in which brooding Crustacea of similar size divide their reproductive output, ie. many small eggs or a few big eggs, it is the capacity of the brood chamber which must be similar.

The amphipod brood pouch is formed by brood plates or oostegites which vary in size and shape (Leite et al., 1986). This is another factor which affects the volume of the brood pouch. Assuming that the eggs are well packed, then brood volume provides a good estimate of the volume of the brood chamber. Therefore to compare how species divide their reproductive output, comparisons must be made for species with the same brood volume.

Warragaia rintouli, which was a smaller amphipod than U. metungi and H. rubra, produced a few small eggs. The smallest mean amphipod brood size reported by Nelson (1980) was 2.4. Therefore in comparison with other gammarideans W. rintouli has small eggs and a small brood (Table 1).

Leucothoe commensalis carried a large number of small eggs compared to other gammarideans (eg. Nelson, 1980). Therefore the hypothesis proposed in the introduction is not supported. Adult mortality risk from predation is thought to be extremely low, and the benign environment within the host with an abundant food supply suggested that adult mortality risk from other factors is small. However, L. commensalis carried many small eggs, perhaps in response to the lack of available hosts. In order to maximize the chance of offspring finding a host when settlement occurs, L. commensalis produced a large number of small eggs. The commensal way of life has reduced the risk of predation for L. commensalis but host availability has imposed other problems that have resulted in a reproductive pattern of many small eggs. This is the first

time this pattern has been found for a commensal amphipod.

(c) Hatchling Size

Although H. rubra has smaller eggs than U. metunqi there is no significant difference in hatchling size for these species ($t = 0.9639$, $df = 42$).

This result has not been reported before and there is a lack of data about egg size and hatchling size despite the fact that it is often claimed that larger eggs produce larger and therefore fitter offspring (Steele and Steele, 1975b; Skadsheim, 1984). These claims seem to be based on the findings of Thorsøn (1950), and the model of Smith and Fretwell (1974) which proposed that as more energy is expended on individual offspring the fitness of the offspring increases. Steele (1983) presented data on egg size and hatchling size in lysianassoid amphipods, however it is not clear whether the data represent species means or individuals. Van Dolah and Bird (1980) argued that larger eggs produced larger young and in the coarse-grained sand environment of infaunal amphipods, large young may be better survivors.

However, the data herein show that larger eggs do not always produce larger offspring.

Why produce a big egg if the hatchling is the same size as that produced from a smaller egg? It is thought that large eggs cost more to produce than small eggs (Grahame and Branch, 1985), and large eggs contain more yolk (Steele and Steele, 1975b) and lipid than small eggs (Herring, 1974). Development time is shorter for small eggs (Steele and Steele, 1975b), but in the infaunal environment of U. metunqi, longer development time may not be a disadvantage and the young would emerge from the brood pouch better nourished. Hyale rubra embryos develop more quickly and receive less nutrition and this may be a consequence of epifaunal life. Van Dolah and Bird (1980) argued that shorter development times would be advantageous for epifaunal amphipods to minimize predation on offspring in the brood pouch. The female may also benefit from carrying the brood for a shorter time in an epifaunal environment. Ovigerous females may be more prone to predation (Winfield and Townsend, 1983), and there is probably an energetic cost in carrying in eggs (Calow,

1979).

(d) Reproductive Effort

Reproductive effort is a measure of the amount of energy that an organism allocates to reproduction (Smith and Fretwell, 1974; Hirshfield and Tinkle, 1975; Pianka, 1978) and the concept is central to any comparison of reproductive patterns among species. It is best measured in units of energy (Hirshfield and Tinkle, 1975) although it is not possible to make direct measurements of reproductive effort and various estimates derived from both energy budgets, and the ratio of brood biomass to body biomass (either as joules or weight) have been used.

I have used the ratio of mean brood volume to mean ovigerous female volume (expressed as a percentage), to estimate reproductive effort. The brood represents the energy expended by the parents and volume is the best measure of female size. The analysis of data in this study has revealed the importance of volume as a measure of female size.

Measures of biomass have rarely been used to estimate reproductive effort in amphipod studies, although Fenwick (1984) calculated the ratio of mean brood dry weight and mean female dry weight. Nelson (1980) used the ratio of brood size to female body length to calculate an index of reproductive effort and Wildish (1982) used the ratio of brood volume to female volume (where volume was calculated using total length and the depth of the third peraeon). Wildish appreciated the importance of a second dimension in defining female size, however, his estimate did not allow for the difference in body mass such as between broad-bodied urohaustoriids and narrow-bodied hyalids.

I found that reproductive effort among the study species varied from 6.5 % for L. commensalis to 12.3 % for H. rubra (Table 1). Hyale rubra is at the greatest risk from predation and would be expected to have greater reproductive effort than the infaunal and commensal species (Hirshfield and Tinkle, 1975). Nelson (1980) also explained the higher reproductive effort of epifaunal gammarids as a consequence of the risk of predation. Reproductive effort was greater for U. metunqi than for W. rintouli. Williams (1966) predicted that small short-lived

species would have greater reproductive effort than larger long-lived species. This result is consistent with Williams' prediction.

Van Dolah and Bird (1980) found reproductive effort to be equal for infaunal and epifaunal amphipods but they measured reproductive effort as brood volume. Nelson (1980) found a significant difference between the reproductive effort of infaunal haustoriids and epifaunal gammarids. Fenwick (1984) measured reproductive effort for the infaunal amphipod Protophoxus australis Barnard (38.07 %) and the epifaunal amphipod Patuki roperi Fenwick (10.80 %). He argued that although the epifaunal habitat of P. roperi was an environment with greater mortality risk than the infaunal habitat of P. australis, "its lower reproductive effort gave greater female survival".

(e) Reproductive Patterns

Van Dolah and Bird (1980) only considered egg size and number when comparing the reproductive patterns of infaunal and epifaunal amphipods. However, there are other traits that must be considered when describing the

reproductive patterns of species. These include age at maturity, reproductive activity, generation time and the number of cohorts produced in one year (Stearns, 1976).

One of the most striking differences between the reproductive patterns of the infaunal amphipods U. metunqi and W. rintouli and the epifaunal amphipod H. rubra was the difference in reproductive activity and its consequences. Both of the infaunal species had continuous reproductive activity with recruitment every season, and there was no season or long period of low population density. Hyale rubra, however, had no reproductive activity throughout winter and recruitment was limited to summer and autumn. Population density was very low throughout winter and into the following spring, and the population depended on a small number of individuals which survived the winter, to produce the fast growing summer recruits. This pattern is also seen in other hyalids (Hiwatari and ~~Barbicornis~~ Kajihara, 1984).

In both the infaunal and epifaunal species, ~~generation time~~ life span and age at reproductive maturity varied with the season of recruitment. All three species had long-lived winter generations and short-lived summer generations

(Table 1). Warragaia rintouli had the shortest ~~generation time~~ life span and reached maturity at an earlier age (for both its long-lived and short-lived generations) than U. metungi and H. rubra. As a consequence, W. rintouli also produced the greatest number of cohorts in a year. Warragaia rintouli is therefore maximizing turnover and this a consequence of small body size. Because it is a small amphipod, W. rintouli cannot carry lots of eggs, either small or large. There is probably a minimum viable egg size (Mauchline, 1988) and species with small eggs, such as W. rintouli need to reproduce more often ie. rapid turnover, to increase fecundity. They cannot opt for more small eggs to increase their number of offspring .

(ii) Life History Theories

(a) Van Dolah and Bird (1980)

Adult mortality risk was considered by Van Dolah and Bird (1980) to be correlated positively with egg number and inversely with egg size. The data herein show that this is not always so. Leucothoe commensalis, with adults living in a benign environment within their host, produced

many small eggs. The epifaunal species H. rubra had smaller eggs than U. metungi but did not have more eggs, and the infaunal W. rintouli had eggs as small those of H. rubra.

Life history patterns have evolved as a compromise between many factors such as egg size, brood size, generation time, age at maturity and frequency of reproduction. These factors cannot be considered in isolation. Egg size and brood size are dependent variables which in turn affect other variables. For example, large eggs take longer to develop than small eggs (Steel and Steele, 1975b), and this in turn influences the number of broods that a female can produce.

In order to make comparisons of reproductive patterns all of these factors must be considered, and it is unlikely that one factor, such as adult mortality risk, will be established as a good predictor of reproductive patterns.

A major problem in the model arises because Van Dolah and Bird's model considers only infaunal and epifaunal

amphipods of the same size. Van Dolah and Bird (1980) used total length as a measure of size for comparing data for standard size females based on regression analysis. This method has limited applicability for interspecies comparison, and total length is not the best measure of size when comparing egg size and number. To compare how species divide their reproductive output, ie. many small eggs versus few large eggs, comparisons must be between species of equal brood chamber capacity. Fenwick (1984) pointed out the difficulty in comparing other traits between species, such as those with determinate and indeterminate growth.

(b) Body Size as a Constraint on Amphipod Life History Strategies

The results of my studies suggest that body size and shape place constraints on life history strategies. In many cases body shape is influenced by habitat and I consider that these are important factors in determining life history patterns. For example, the narrow elongate body of tube dwelling amphipods such as the corophioid Cerapus puts entirely different constraints on brood

volume than the broad fusiform body of fossorial urohaustoriids and haustoriids. Small amphipods, such as W. rintouli, don't have the "choice" of a few large eggs or many small eggs because there is probably a minimum viable egg size (Mauchline, 1988). A large amphipod like L. commensalis could theoretically vary both its eggs size and egg number, and balance other factors such as the consequences of short and long egg development times.

In recent life history studies, body size has been investigated as a factor in the evolution of life history patterns. Barbault (1988) considered that body size imposed constraints on many traits including brood volume, energetic needs and vulnerability to certain predators. Stearns (1983, 1984) examined the effect of size and phylogeny on patterns of covariation in life history traits of mammals and lizards and found that morphology and size may constrain life history evolution. In brachyuran crabs, female body size was the principal determinant of reproductive output, and Hines (1982) argued that allometric constraints meant that brachyuran life history traits were not "free to evolve under purely demographic forces". The constraints that Hines (1982)

envisaged were both energetic constraints and constraints imposed by the brachyuran body cavity. The constraints on amphipod life history strategies are imposed by body size and shape, and concomitantly the volume of the brood chamber.

Steele (1983) also considered body size to be an important factor in amphipod life history strategies. He argued that small size was an advantage in the tropics where fecundity could be increased by rapid turnover in environments where there are long periods of food availability. In cold environments where food was only available for short periods, large size was advantageous because a large single brood could be produced.

Southwood (1977, 1988) developed the idea that habitat is the templet "on which evolution forges characteristic life history strategies". He defined habitats in terms of axes of frequency of disturbance and level of adversity, and predicted different tactics for habitats at various points on the axes. However, in addition to the selection pressures described by Southwood's axes, habitat imposes constraints on the life history tactics of amphipods

through selection for morphology and size. A broad, fusiform body is an advantage for a fossorial amphipod like U. metunqi and this body shape creates a larger brood chamber than for narrow-bodied amphipods of the same length.

Hyale rubra has small eggs and this is advantageous in a habitat where there is a risk of predation and when reproduction is seasonal. Small eggs allow rapid development and increased fecundity through more generations being produced in the reproductive season. The eggs of H. rubra are probably approaching the minimum viable size for amphipod eggs (Table 1) and brood size is therefore determined by the requirement to have small eggs. There may be constraints on the size of H. rubra in the epifaunal environment where protection is found among the algae.

Warraqaia rintouli is a small amphipod with a small brood of small eggs, a short generation time and early maturity. Because W. rintouli is a small species, both egg size and brood size are small. These reproductive traits are constrained by body size, and fecundity is increased

by short generation times and rapid turnover.

Urohaustorius metunqi had the largest eggs in the study but compared with other gammarideans, the eggs are not large. It is a broad fossorial amphipod which burrows by passing sand grains between its legs, so there are constraints on its size. It is able to carry large eggs because it is broad-bodied and in the infaunal environment there is probably no disadvantage in slow development.

Leucothoe commensalis is the largest amphipod in the study and it has a large brood of small eggs. Prior to this study commensal amphipods were thought to have small brood sizes, however L. commensalis has a large brood in response to the unavailability of hosts. In order to maximize brood size, L. commensalis has small eggs.

Van Dolah and Bird (1980) proposed that amphipod life history patterns could be predicted by adult mortality risk, and there have been many other attempts to find factors which are reliable predictors of life history strategies. It seems unlikely that a single factor will be found to be a reliable predictor of life history patterns,

and this study and other recent work (Hines, 1982; Steele, 1983; Stearns, 1983 and 1984; Barbault, 1988) show the need to consider the constraints that body size imposes on life history evolution.

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Table 1. Life history traits for gammaridean amphipods Hyale rubra, Leucothoe commensalis, Urohaustorius metungi and Warragaia rintouli. L = long-lived generation, S = short-lived generation.

	Hyale rubra	Leucothoe commensalis	Urohaustorius metungi	Warragaia rintouli	Nelson (1980) Range
Mean brood size	5.49	99.3	4.72	1.94	2.4 - 407.0
Mean egg size (mm)	0.34	0.42	0.51	0.33	0.30 - 1.75
Brood volume (mm^3)	0.1131	3.96	0.3525	0.0378	2.4 - 40.8
Mean length ovig female (mm)	3.65	15.82	3.50	2.00	
Mean volume ovig. female (ml x 10^{-3})	0.92	61.0	3.64	0.33	
Mean hatchling size (mm)	0.96	1.50	0.96	0.56	
Reproductive effort %	12.3	6.5	9.7	11.5	
Number of cohorts Jan - Dec 1982	5	-	5	7	
No. simultaneous cohorts	3 - 5	-	2 - 5	3 - 6	
Brood mortality	ns	-	ns	32.5%	
Mean longevity					
L (days)	345	-	231	227	
S (days)	133	-	181	123	
Mean age at female maturity					
L (days)	170	-	145	76	
S (days)	40	-	58	34	
Reproductive activity	seasonal	continuous	continuous	continuous	